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Male inflorescence of, l to r, *Zea diploperennis*, *Z. perennis*, and *Z. luxuria*

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NONFLYING MAMMAL POLLINATION OF SOUTHERN AFRICAN PROTEAS: A NON-COEVOLVED SYSTEM[1]

DELBERT WIENS,[2] JOHN P. ROURKE,[3] BRENDA B. CASPER,[4] ERIC A. RICKART,[2] TIMOTHY R. LAPINE,[2] C. JEANNE PETERSON,[2] AND ALAN CHANNING[5]

ABSTRACT

Traits characterizing those proteas adapted for pollination by nonflying mammals include: bowl-shaped heads bearing fleshy bracts, these borne on short, flexible peduncles, often at or near ground level (geoflorous) and hidden beneath dense overlying foliage (cryptic), and producing copious nectar (ca. 1.8 ml/head, standing crop); individual florets with wiry, yet flexible styles and a nectar-stigma distance of 10 mm; a distinctive yeastlike odor; nocturnal anthesis; sucrose-rich nectar with a high total carbohydrate content (ca. 36%) and a relatively low proportion of amino acids. Evidence of small-mammal visitation to protea flowering heads includes: the presence of pollen on the rostra (carried in a position to effect pollination when foraging for nectar); the transport of fluorescing powders to flowering heads both within and between plants; the accumulation of small-mammal feces in flowering heads, and the destruction of exclosure bags containing nectar-rich heads. The period of greatest small-mammal activity (1800 hr.) coincides with maximum flower opening. T maze experiments showed that small mammals, when given a choice between typically bird-pollinated proteas and those having characteristics of flowers pollinated by nonflying mammals, always foraged on the latter. That small mammals can effect pollination is indicated by their foraging behavior on flowering heads while in captivity, the morphological "fit" between individual florets and the rostra of small mammals, and by selective exclosure experiments that reduced seed set (50% and 95%) when small mammals were excluded and visitation was limited to insects (mostly honey bees). The nectar produced

[1] The study was supported in part by NSF grant (DEB 78-11624). We thank B. Albee, L. Arnow, H. G. and I. Baker, P. Cox, V. Grant, S. D. Hopper, P. H. Raven, and V. Turner for helpful comments on the manuscript.

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by these proteas meets the energy requirements of the small-mammal community for only several days annually, thus coevolution is impossible. Proteas adapted for pollination by nonflying mammals have evolved unilaterally, probably from bird-pollinated prototypes, possibly in response to progressive decrease in population size. Recent discoveries in the Neotropics of flowers with some similar characteristics and also pollinated by nonflying mammals support the existence of a worldwide class of flowers adapted for such pollinators.

The pollination of flowers by nonflying mammals was first mentioned by Kerner (1895, v. 2, p. 230) and was discussed nearly 50 years ago by Porsch (1934, 1935, 1936a, 1936b). The subject was not given further attention, however, until Morcombe (1968) suggested pollinatory relationships between various proteaceous flowers and nonflying mammals in the southwestern Australian flora. Rourke and Wiens (1977) reviewed the problem and noted that various floral features convergent in Australian and South African Proteaceae suggested adaptations for pollination by nonflying mammals. The following year Wiens and Rourke (1978) offered substantive evidence for pollination by nonflying mammals (mostly rodents) in two species of South African proteas. Two previous studies of presumably bat-pollinated African plants, viz., the baobab (Bombacaceae) (Coe & Isaac, 1965) and *Maranthes* (Chrysobalanaceae) (Lack, 1977) demonstrated visitation and nectar feeding by bush babies (*Galago crassicaudatus* Geoffroy) and genets (*Genetta tigrina* Schreber), respectively. Recent interest in the subject has resulted in a number of publications: Sussman and Raven (1978) reviewed the problem and reported pollination by arboreal Madagascan mouselike lemurs; Sleumer (1955) and Carpenter (1978a) reported evidence for the pollination of eastern Australian banksias by sugar gliders (*Petaurus breviceps* Waterhouse) and the indigenous placental bushrat (*Rattus fuscipes* Waterhouse), respectively. Holm (1978) and Ford, Paton, and Forde (1979) commented on the problem and Armstrong (1979) reviewed the subject for Australia generally. Wiens, Renfree, and Wooller (1979) and Hopper (1980) studied the pollination of *Banksia* and other flowers by the southwestern Australian marsupial honey possum (*Tarsipes rostratus* = *T. spenserae* Gray). In the New World, Prance (1980) observed probable pollination by cebus monkeys; and Janson, Terborgh, and Emmons (1981) reported extensive visitation and apparent pollination in Bombacaceae and Combretaceae in the Amazon by monkeys [including the small (100 g) pigmy marmoset], opossums, and procyonids. Lumer (1980) observed pollination of *Blakea* (Melastomataceae) by rodents in Costa Rica, and Steiner (1981) discovered probable pollination by opossums in *Mabea* (Euphorbiaceae) in Panama. The suggestion of rodent pollination in Hawaiian *Freycinetia* (Degener, 1945) is apparently in error (Cox, 1981).

We report the results of three seasons of field studies on several species of southern African species of *Protea* (Proteaceae) with characteristics indicating adaptations for nonflying mammal pollination (hereafter referred to as NMP proteas), as contrasted to proteas with features showing adaptations for bird pollination (BP proteas) (Wiens & Rourke, 1978). Whenever possible the two systems are compared. These observations cover the winter–early spring (August–September) field seasons of 1978–79 and the summer (February) field season of 1980 in the Cape region of South Africa. Wiens and Rourke (1978) established that several murid rodents and a few additional small mammals visited the flowering heads of *Protea amplexicaulis* (Salisb.) R. Br. and *P. humiflora* Andr., as evidenced by the presence of protea pollen loads on the rostra of captured animals. They further demonstrated that the flowers and small mammals possessed the respective structural and behavioral features to effect pollen transfer, and that several rodents foraged readily and non-destructively on the nectar from flowering heads of several proteas while in captivity.

This study has two broad objectives: first, to test further the proposition that these flowers are pollinated by nonflying mammals and to gain a general understanding of how the pollination system functions as an integrated whole; and secondly, to consider why this unusual animal-flower relationship may have evolved. Specific areas of study included: (1) the general nature of the plant association in which NMP proteas occur, (2) the composition and activity patterns of the associated small-mammal community, (3) the temporal patterns of anthesis, nectar secretion, and odor production, (4) nectar volume, total sugar content, carbohydrate and amino acid composition, (5) stylar and general floral struc-

TABLE 1. The number of small mammals examined for pollen loads and the proteas with which they were associated.

Protea	Small Mammal					Study Site
	Acomys subspinosus	*Aethomys namaquensis*	*Elephantulus edwardii*	*Praomys verreauxi*	*Rhabdomys pumilio*	
P. amplexicaulis[c,d]	15	31[a,b]	2	3	16[a]	Jonasplaats, see text
P. cryophila[c]	1[a]	2	5			Sneeubergnek, Cedarberg Mts., E of Citrusdale
P. effusa[c]		1	3	2	4	East bench, Murray Farm, above Gydo Pass N. of Ceres
P. humiflora[c,d]	13[b]	16[a,b]	2[a,b]	3[a]	14[a,b]	Jonasnek
P. recondita[c]		3	3[b]	2	4[b]	Same as *P. effusa*
P. restionifolia		3[a]				Pocskraal, N. shore Stormsvlei reservoir, S. of Worcester
P. scabra		[a]				W. of Villiersdorp
P. sulphurea		2[a,b]			1[b]	W. of Ouberg Pass, NE of Montague

[a] Captive animals of this species foraged on flowering heads of the respective protea in a manner to assure effective pollination.

[b] Animals with numerous protea pollen grains (>100 and often >1,000) in fecal samples taken directly from the colon.

[c] Some heads of these protea species contained fecal pellets.

[d] In addition to the animals listed, single specimens of *Crocidura* sp. and *Graphiuris ocularis* were trapped around *P. amplexicaulis* and one *Dendromus melanotis* and a *Mus minutoides* were captured in *P. humiflora* stands.

ture, (6) genetic compatibility and pollen viability, (7) the energy resources protea nectar provides to the small-mammal community, and (8) the relative importance of insects as pollinators of NMP proteas.

RESEARCH AREAS AND SPECIES STUDIED

The NMP proteas utilized in this research are endemic to the southwestern Cape flora (fynbos) of South Africa. This vegetation is unique, with (1) exceptionally rich species diversity (ca. 8,850 species) and high endemism (73.1%), (2) adaptations for periodic burning, (3) a virtual absence of indigenous trees, (4) a low percentage of annuals, and (5) restriction to the Table Mountain Sandstone, which is highly depauperate nutritionally especially for P and N. Uplift and erosion of this formation have produced a highly dissected landscape comprised of many small mountain ranges with diverse elevations, precipitation, and soils. Predictably, numerous species exist only as small populations and in isolated habitats (Goldblatt, 1978; Taylor, 1978; Kruger, 1979).

Although the vegetation is unique, the animal community is not. The small-mammal community, for example, is composed largely of species with ranges extending far beyond the distribution of the Cape flora. Likewise, the bee fauna is not especially noteworthy (Michener, 1979), although bee-pollinated plants such as legumes constitute an important element of the flora (Goldblatt, 1978).

The NMP protea study sites are indicated in Table 1. BP proteas used for comparative purposes included *P. arborea* Houtt., *P. laurifolia* Thunb. (both from Jonasnek), and *P. repens* (L.) L. (from Jonasplaats, see section on *P. amplexicaulis*). These proteas are illustrated in Rourke (1980).

PROTEA HUMIFLORA AND *P. AMPLEXICAULIS*

Protea humiflora was studied during late winter–early spring (mid-August to mid-September) 1978–79 on Jonaskop, a prominent mountain in the Riviersonderendberge, approximately 50 km south of Worcester and 100 km east of Cape Town. On Jonaskop, *P. humiflora* forms dense stands along a restricted access road to the summit. Two adjacent study sites (A and B), each

TABLE 2. Density, species composition, and composite home range data from live trapping grids in stands of *Protea humiflora* at Jonasnek.

Species	1978 Site A Number of Ind.	1978 Site A Number/Hec.	1978 Site A % Comp.	1978 Site B Number of Ind.	1978 Site B Number/Hec.	1978 Site B % Comp.	1979 Site B Number of Ind.	1979 Site B Number/Hec.	1979 Site B % Comp.	Adjusted Home Range Length (m) N	$\overline{X}$	Range
Acomys subspinosus	1	5	2.6	20	95	35.1	7	33	35.0	5	39.3	(35.0–47.5)
Aethomys namaquensis	1	5	2.6	13	62	22.8	12	57	60.0	6	46.2	(27.5–58.0)
Praomys verreauxi	11	52	28.9	4	20	7.0	—	—	—	4	35.4	(27.5–45.5)
Rhabdomys pumilio	25	119	65.8	17	81	29.8	1	5	5.0	17	37.8	(25.0–58.0)
Elephantulus edwardii	—	—	—	3	14	5.3	—	—	—	3	34.6	(27.5–44.2)
Totals	38	181		57	272		20	95				

approximately 2,100 m^2, were selected along this road at approximately 700 m (hereafter referred to as Jonasnek). During the 1978 field season the species composition, frequency, and cover were determined for the perennial plants on sites A and B. Both sites were divided into 10 m^2 quadrats, each plant was identified and its position and cover plotted on graph paper and the location of each Sherman trap noted.

Various observations were also made on *P. amplexicaulis* at somewhat higher elevations on Jonaskop (ca. 1,000 m) in an area known locally as Jonasplaats. This locality is relatively flat with many scattered individuals of *P. amplexicaulis* occurring along the east side of the access road (the west side of the road was burned in 1976).

SMALL-MAMMAL TRAPPING SYSTEM

METHODS

At the *P. humiflora* study sites at Jonasnek a square grid of 100 Sherman live traps [45 × 45 m (2,025 m^2), approximately 5 m trap distances] was used to establish the species composition, activity, and movement patterns of the small-mammal community. Each trap was fitted with a switch mechanism and wired to a portable Esterline-Angus 20 Channel event recorder that indicated exact capture times and trap positions within the grid. This system facilitated rapid trap checking while minimizing human disturbances to the grid area. Traps were baited with rolled oats and peanut butter and checked at sunrise, sunset, and at variable intervals of 2 to 8 hours over a 24-hour period. Upon initial capture, animals were identified, weighed, sexed, checked for pollen load, marked with numbered ear tags (or toe-clipped), and released at the point of capture. The times and positions of recaptures were merely recorded, but animals were occasionally rechecked for pollen load. Rickart (1981) provides further details. Small mammals associated with the other proteas listed in Table 1 were captured in Sherman live traps (occasionally snap traps) set in irregular transects around, under, or on the branches of flowering proteas.

During the 1978 season, the grid system was operated successively at two sites. The first (Jonasnek A) consisted of a relatively level area and the second (Jonasnek B) was on an adjacent, rocky, north-facing, 25°–30° slope (the warm, dry slope in the southern hemisphere) approximately 100 m from site A. Vegetation was qualitatively similar on both sites, each having the same 34 species dominated by dense stands of *P. humiflora* and scattered individuals of *Leucodendron salignum* R. Br., with generally similar densities of herbaceous ground cover. Soil development was more extensive, however, on site A. The grid was run continuously in 1978 for 121 hours at

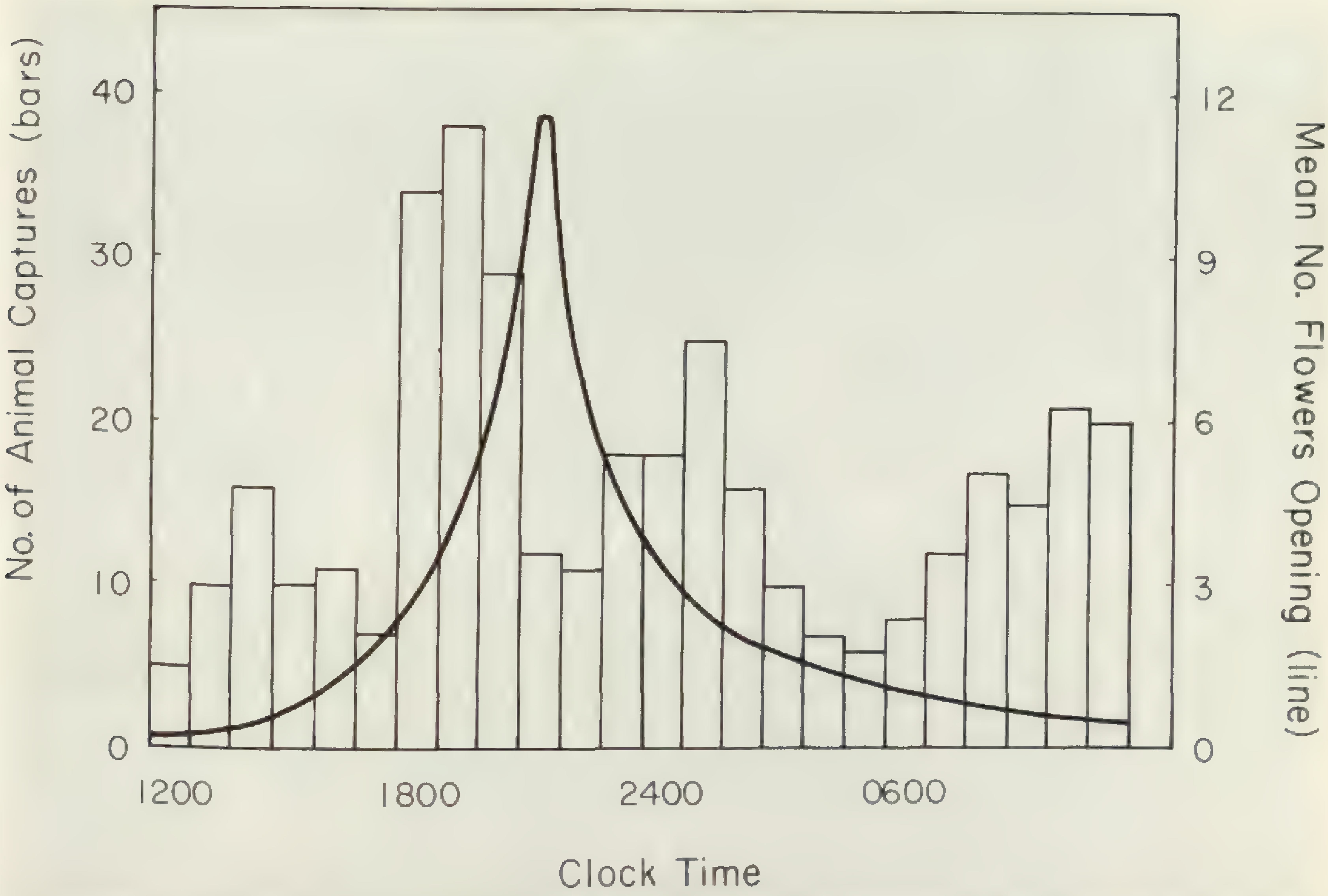


FIGURE 1. Cumulative activity patterns of all five small mammals occurring on the Jonasnek study sites (histograms) and the opening patterns of *P. humiflora* flowers (line).

site A and 193 hours at site B. In 1979 the grid was operated only at site B for a total of 355 hours. By the end of each trapping period, fewer than 5% of the animals captured during a 24-hour period were unmarked.

RESULTS

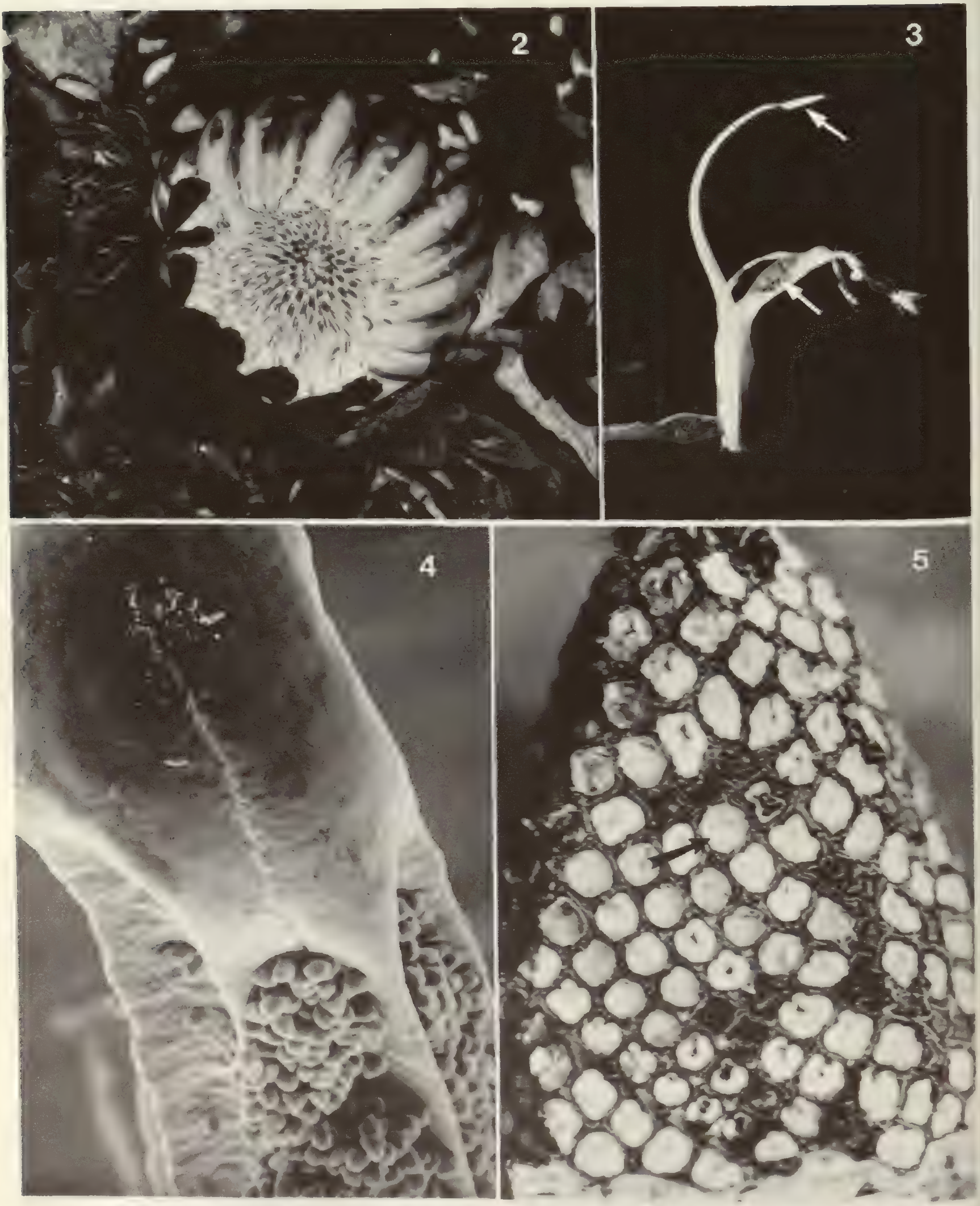
The grid-trapping data are summarized in Table 2. The 1978 data show considerable differences in species composition between the two grid sites, suggesting that microgeographic variation affects the species composition of the small-mammal community within individual stands of *P. humiflora.* The data from 1979 also show a profound reduction in overall densities on site B. Only densities of the Namaqua rock mouse (*Aethomys*) appeared unchanged, while Verreaux's mouse (*Praomys*) and the elephant shrews (*Elephantulus*) were absent. *Praomys* was not recorded anywhere in the study region the second year.

Mean home ranges for the various species were estimated from recapture data by calculating adjusted range length (distance between the farthest two points of capture plus the average inter-trap distance of 5 m) for individuals with five or more captures (Table 2). These values are probably underestimated because they approach the dimensions of the grid, which were relatively small for this purpose, particularly with respect to the Cape striped field mouse (*Rhabdomys*) and *Aethomys.* Figure 1 shows the cumulative activity pattern determined from capture times of individuals of all five species. Because some of the captures were probably artifacts due to the quick retrapping of previously released animals, recaptures that occurred less than one hour after the release were eliminated from the histogram. The diurnal activity shown is almost exclusively due to *Rhabdomys.* The remaining species are predominantly nocturnal. Of the 376 total captures, 232 (61.7%) occurred during the nocturnal-crepuscular period from 1800 to 0700 with highest activity levels occurring just after dusk.

FLORAL MORPHOLOGY OF NMP PROTEAS

PROTEA AMPLEXICAULIS—A TYPICAL NMP PROTEA

The inflorescence is a many-flowered, bowl-shaped head surrounded by dark, fleshy invo-



FIGURES 2–5. Floral and fruiting features of *P. amplexicaulis* and *P. humiflora*.—2. Flowering head (*P. a.*)—3. Individual floret, arrows indicate pollen presenter and nectar reservoir (*P. a.*)—4. SEM photo of style tip showing stigmatic slit and grooves of the pollen presenter region (*P. a.*) (× ca. 200).—5. Fruiting head with pistils cut transversely to expose sterile ovaries and those containing endosperm (arrow) (*P. h.*).

lucral bracts (Fig. 2). The peduncle is stout and short (3–4 mm), yet flexible, the heads appearing sessile along the branches. The heads are often borne near ground level (geoflorous) and are typically deeply hidden beneath dense, overlying foliage (cryptic). The heads are similar to *P. humiflora* in appearance and habit, but are generally more cryptic.

The individual flowers (florets) comprising protea heads are unusual (Fig. 3). The uniovulate pistil is surrounded by four dull-white, non-showy perianth segments, each bearing a single, sessile anther. The unique feature of the floret, however, is the extremely wiry, yet flexible style, which readily withstands rough treatment. It has the dual function of pollen dispersal and reception. Pollen is deposited prior to anthesis onto a specialized, longitudinally grooved, apical region of the style known as the pollen presenter (Fig. 4). Although pollen covers most of the distal portion of the style, it does not initially reach the stigma itself, this being a highly reduced microscopic groove at the apex of the style (Fig. 4). Physical transfer of pollen is thus necessary even for self-pollination (see section on Genetic Compatibility). Stylar presentation of pollen also occurs in Asteraceae and the Campanulales, but the details differ.

In proteas the base of the style ruptures the lower perianth segments as it grows laterally from the perianth envelope during late bud development. Eventually only the base of the style and the pollen presenter remain enclosed by the perianth segments and the surrounding anthers. The rest of the style forms a bowlike structure outside the perianth just prior to anthesis (Rourke, 1980). Nectar secretion occurs at this time (see section on Nectar Production). Although anthesis, i.e., the emergence of the pollen presenter from the enfolding anthers and perianth segments, is mildly explosive, the pollen, because it is sticky, is not dislodged from the pollen presenter. In *P. amplexicaulis* and other NMP proteas examined, the three united perianth segments form a nectar reservoir about 10 mm below the stigma (Fig. 3). Because the flowers are in close proximity, however, the nectar often pools, particularly around the bracts.

ADAPTATIONS OF PROTEA FLOWERS FOR POLLINATION BY NONFLYING MAMMALS

The basic floral structures of proteas inferring pollination by nonflying mammals were summarized by Wiens and Rourke (1978) and discussed and compared to Australian Proteaceae by Rourke and Wiens (1977). These structures as illustrated for *P. amplexicaulis* include: (1) bowl-shaped heads borne on short (3–4 mm), stout peduncles, often with the outside of the bracts dark-colored, (2) copious, sucrose-rich nectar production with a high (36%) total carbohydrate composition, (3) often inflexed, wiry styles ca. 30–40 mm long, (4) cryptic, geoflorous, axillary positioning of the heads, and (5) a distinctive "yeasty" odor. In contrast, BP proteas produce (1) cylindrical heads with brightly colored bracts, (2) copious, hexose-rich nectar with a low (20–25%) total carbohydrate composition, (3) straight styles ca. 60–90 mm long, (4) conspicuous, brightly colored, terminally borne heads, and (5) no obvious odor.

The following proteas should be added to those previously suggested by Rourke and Wiens (1977) as exhibiting morphologies consistent with nonflying mammal pollination: *P. caespitosa* Andr., *P. convexa* Phill., *P. cryophila* Bolus, *P. denticulata* Rourke, *P. effusa* E. Mey. ex Meisn., *P. pendula* R. Br., *P. piscina* Rourke, *P. pruinosa* Rourke, *P. recondita* Buek ex Meisn., *P. roupelliae* Meisn., *P. tenax* (Salisb.) R. Br. The following species should be deleted: *P. lorea* R. Br., *P. scorzonerifolia* (Salisb. ex Knight) Rourke.

Many NMP proteas do not have cryptic heads although they are geoflorous, (e.g., *P. cryophila*), while one is cryptic but not geoflorous (*P. recondita*). Some proteas that are neither cryptic nor geoflorous [e.g., *P. nana* (Berg.) Thunb., *P. pityphylla* Phill., *P. pudens* Rourke, *P. witzenbergiana* Phill.] may also be pollinated by nonflying mammals, but verification is needed. Straight, as well as inflexed, styles probably also occur in many presumably NMP proteas; but the relatively short styles (ca. 30–50 mm) that maintain an effective stigma-nectar distance of about 10 mm are probably most important for a functional rostrum-stigma "fit" (Wiens & Rourke, 1978).

Protea cryophila is an impressive exception to the short-style character, yet it appears to prove the rule. Although the styles are ca. 80–90 mm long, the nectar secreted in mature buds is not retained at the point where the style arches out of the perianth tube, as occurs in *P. amplexicaulis* or *P. humiflora*. Instead, the tube is filled with nectar for about 70–80 mm up the tightly stretched perianth tube and approximately 10 mm below the stigma. At this point the tube ends and the perianth flattens out into a strap-shaped structure across which the nectar does not migrate, and where it subsequently forms a nectar droplet. A captive spiny mouse (*Acomys*), when presented with a head of *P. cryophila*, foraged for nectar among mature buds at this level and contacted previously opened stigmas. Thus the critical stigma-nectar distance of ca. 10 mm is maintained.

The structure of the nectar reservoir in *P. am-*

plexicaulis and *P. humiflora* may also be important in pollination. In these species it forms a shallow, "troughlike" structure (Fig. 3), which could facilitate nectar lapping by small mammals. In a BP protea (e.g., *P. repens*) the nectar reservoir, by contrast, resembles a well at the base of the style into which a bird's beak or tongue could be readily inserted and the stigma-nectar distance ratio approximates the length of the entire style (and also the length of the pollinating bird's beak and extensible tongue).

The cryptic positioning of the heads in a number of NMP proteas needs further description. Different strategies are involved: (1) *interior cauliflory*—heads generally borne along older stems densely covered with overlying shoots (*P. amplexicaulis, P. humiflora*); (2) *interior geoflory*—heads borne at or very near ground level and generally covered with overlying shoots, especially in older plants [*P. cordata* Thunb., *P. subulifolia* (Salisb. ex Knight) Rourke]; (3) *interior penduly*—heads borne on pendulous branches generally hidden by overlying shoots, with heads often drooping to near ground level (*P. sulphurea* Phill., *P. witzenbergiana* Phill.); (4) *exterior terminal*—heads enclosed by large surrounding bracts (*P. recondita, P. foliosa* Rourke).

Why crypsis evolved is unclear; but a possible explanation is the reduction of occasional nectar robbing by flower birds that presumably cue visually. Dr. E. Granger (pers. comm.), however, suggests that crypsis might reduce predation on small-mammal pollinators by nocturnal raptors (owls), of which there are a dozen species in southern Africa (Oatley, 1971). Small mammals foraging on exposed flower heads should be more vulnerable to aerial predation than animals foraging inside a foliage cover. These four forms of crypsis also occur in the proteaceous genera *Banksia* and *Dryandra* of Australia (George, 1981), which also has a large owl fauna (Morcombe, 1974).

Stigma Morphology

METHODS

Because of its reduced nature, the stigma morphology of the NMP proteas *P. humiflora* and *P. amplexicaulis* and the BP proteas *P. cynaroides* (L.) L. and *P. repens* was studied with a Hitachi 450 scanning electron microscope to determine whether its structure might provide evidence relating to more efficient pollination by particular animals. Proteaceae are generally protandrous and we suspected there might be differing periods of slit opening or receptivity. Seven specimens were collected every 3 hours for a period of 24 hours. Both individual flowers and entire flowering heads were collected at each sampling, and special care was taken not to disturb the flowers prior to fixation.

Styles were fixed for 24 hours in one of the following: (1) liquid nigrogen (N_2), (2) supercooled 95% ETOH, (3) a mixture of 50% formalin and 95% ETOH, or (4) a solution of magnesium phosphate ($MgPO_4$). Styles of individual flowers were prepared by one of the following methods: air dried directly after removal from the fixative, washed in 95% ETOH prior to drying, or processed with a critical point drier. These different methods of fixation and drying produced no detectable changes in stylar structure. Stigmatic morphology was compared among flowers (1) fixed at different times of the day, (2) occurring at varying positions on the flowering head, and (3) representing different age classes.

RESULTS

Observation of approximately 300 stigmas of *P. humiflora* and 200 stigmas from the other species (see above), plus *P. minor* (Phill.) Compton, produced little or no evidence that the stigmatic slit ever opened to any appreciable degree (Fig. 4). Neither did we observe structural changes suggesting differing cycles of receptivity, nor evidence indicating differential pollination success by a certain group of pollinators. Nonetheless, further studies of this subject might prove interesting.

Temporal Patterns of Anthesis and Nectar Production

METHODS

To learn whether anthesis and nectar production are correlated with the activity patterns of small mammals, we determined the time of flower opening for *P. humiflora* under field conditions by counting and marking the number of newly opened flowers at the Jonasnek site A. Flowers on six heads were counted at three-hour intervals over a period of nine days. The erect styles that identify open flowers were marked with red fingernail polish at each time check. Field observations to determine time of flower opening were also made for *P. amplexicaulis* at Jonasplaats and for *P. cryophila* at the Sneeuberg site, but at different time intervals.

TABLE 3. $\bar{X}$ No. flowers opening/head between prescribed time intervals for nonflying mammal and bird pollinated proteas.

Species	Pollination System	0800–0900	1700–1800	2100–2200
P. amplexicaulis	NMP	5.4 (N = 24)	2.6 (N = 24)	9.5 (N = 24)
P. cryophila	NMP	47.4 (N = 50)	4.9 (N = 40)	—
P. effusa	NMP	9.5 (N = 31)	4.0 (N = 34)	—
P. recondita	NMP	8.0 (N = 4)	3.5 (N = 4)	—
P. sulphurea	NMP	22.6 (N = 46)	6.2 (N = 48)	—
P. arborea	BP	19.3 (N = 26)	5.2 (N = 48)	15.7 (N = 26)
P. laurifolia	BP	9.7 (N = 28)	8.0 (N = 33)	3.7 (N = 27)
P. repens	BP	0.36 (N = 22)	12.8 (N = 23)	1.1 (N = 22)

Additional observations on *P. effusa, P. recondita,* and *P. sulphurea,* were made under laboratory conditions, at room temperature, and without special lighting regimes. Flowering heads, which recover easily from wilting and maintain flowering function for a number of days following removal from the plant, were stored in closed plastic bags for 24–48 hours, after which we placed the peduncles in water and cut away the erect styles of open flowers with scissors. Observations were made at 12-hour intervals and the styles of newly opened flowers cut away after each observation. In addition to NMP proteas, three BP proteas (*P. arborea, P. laurifolia, P. repens*) at the Jonasnek and Jonasplaats sites were studied for comparative purposes.

We measured nectar under a dissecting microscope from freshly picked flowering heads using a 15 μl capillary tube. Magnification was necessary to ensure that the nectar droplets from the tightly grouped florets had not pooled.

RESULTS

Time of Anthesis

Protea humiflora clearly shows a maximum rate of flower opening between 1800 and 2100, which is also the period of maximum small-mammal activity (Fig. 1). Other species of NMP proteas also exhibit a primarily nocturnal anthesis, but the periods cannot be bracketed as precisely because the observations were not regularly made at short intervals as in *P. humiflora* (Table 3). *Protea amplexicaulis,* however, would appear to have a pattern of anthesis similar to *P. humiflora,* and judging by casual observations of NMP proteas made during the evening hours, it seems likely this is a general pattern.

Among BP proteas (Table 3), *P. repens* has a midday flower-opening pattern, whereas in *P. laurifolia* Thunb. more florets open in the early morning (0930) and also between 1800 and 2100. The actual time at which anthesis occurred in the newly opened flowers observed at 0930 is unknown because data are lacking for the critical periods (Table 3).

Protea arborea appears to have a largely noctural anthesis, for which we have no apparent explanation. Presumably the species is pollinated by the Cape sugar bird, as are the other two BP species. No sugar birds were ever observed on *P. arborea* in the study areas, however, they were common in nearby (ca. 1 km) stands of *P. laurifolia.*

Nectar Production

No nectar production could be detected in the heads of *P. humiflora* utilized for determining periods of anthesis. Nor were there consistent patterns of nectar production noted in any of the heads on the study areas. A few scattered observations, however, provide some information. Freshly secreted nectar was observed in *P. humiflora* flowers on three separate days (Aug. 16, 26, 30) between 1630 and 1800 hours. These days were relatively cold, windy, and generally stormy, but were without rain during the previous 12 hours. These preliminary observations suggest that nectar secretion is initiated in *P. humiflora* in late afternoon or early evening during periods of relatively low daily temperature and just prior to the period of greatest small-mammal activity.

What appeared to be freshly secreted nectar was also observed in *P. cryophila* at 2030 hours on Feb. 13, but secretion was confined to relatively few flowers on a single head among the 10 under observation. In this instance, however, the

TABLE 4. Total sugar content of nectar (g solute/100 g solution) from nonflying mammal and bird pollinated proteas.

Species	Pollination System	$\overline{X}$ Total Sugar Content	N	S.D.	Range
P. amplexicaulis	NMP	37.2	42	6.3	27.9–47.9
P. cryophila	NMP	33.3	13	7.2	25.2–49.4
P. humiflora	NMP	37.8	59	6.9	28.2–65.4
P. arborea	BP	18.8	5	—	16.8–20.4
P. laurifolia	BP	24.4	20	1.0	20.3–26.6
P. magnifica	BP	20.6	16	2.9	16.2–24.8
P. repens	BP	18.8	45	1.8	14.6–23.6

day was sunny and warm as is common during midsummer.

In *P. angustata* R. Br., *P. cryophila,* and *P. humiflora* nectar was first secreted from mature buds, i.e., while the pollen presenter was still enclosed by the perianth segments, although the style had generally already arched laterally away from the perianth over most of its length. This should not impede pollination, however, because the incurved styles of open flowers easily contact the rostra of small mammals foraging for nectar among the outer few whorls of mature buds. Following warm days, however, the nectar reservoirs of some previously opened flowers in *P. amplexicaulis, P. cryophila,* and *P. humiflora* appeared to develop a moist film by 2000 hours, but no obvious nectar build-up was observed. Laboratory studies such as those by Cowling (1978) may be necessary to obtain an adequate understanding of temporal patterns of nectar secretion.

NECTAR COMPOSITION

METHODS

The nectar of NMP and BP proteas was analyzed for (1) total sugar content (g solute/100 g solution), (2) percentage of different sugars comprising the carbohydrate fraction, and (3) amino acid content. The nectar was extracted from the heads with a capillary tube and the total sugar content was measured with an AO Goldberg refractometer (Model 10923) corrected for temperature. Because of the high total sugar content of NMP protea nectar, it was often diluted with appropriate parts of distilled water in order to retain the value on the refractometer scale. The values were then corrected by the appropriate dilution factor. Only apparently freshly secreted nectar was used for identifying the major components of the carbohydrate fraction and the amino acid content. Nectar for these analyses was immediately spotted on Whatman #1 filter paper, quickly dried, and later chromatographed by I. and H. G. Baker following methods they previously described (Baker, Opler & Baker 1978; Baker & Baker, 1979). Considerable care was taken to reduce the possibility of pollen contamination in the samples used for determining amino acid content. Because freshly secreted nectar was rarely available for analysis of total sugar content, nectar that had accumulated in older heads was utilized. Since nectar remaining in older flowers is more variable than that freshly secreted, the sample size was increased.

RESULTS

Total sugar content of nectar. The three NMP proteas analyzed all have nectar with total sugar content in the mid-thirties ($\overline{X}$ = 36.1%) (Table 4). The four BP proteas have nectar with total sugar content ranging from the high teens to mid-twenties ($\overline{X}$ = 20.7%), which is typical for most bird-pollinated flowers. There is virtually no overlap in the values between the two BP proteas and the NMP proteas and the differences are statistically highly significant ($P \ll .01$). The difference in total sugar content of the nectar in the two groups should be an important distinguishing feature between BP and NMP proteas.

Carbohydrate composition. The nectar of NMP proteas are generally "sucrose-rich," i.e., the ratio of sucrose to glucose-fructose is >0.5 (Baker & Baker, 1979) (Table 5). Thus all the NMP proteas analyzed for carbohydrate composition may be characterized as sucrose-rich, with the exception of *P. angustata* (0.326) which

TABLE 5. Carbohydrate composition (mean proportions) in nonflying mammal and bird pollinated protea nectar.[a]

Species and Pollination Type	Melezitose	Maltose	Sucrose	Glucose	Fructose	Ratio (Sucrose/ Glu + Fru)
P. amplexicaulis (NMP)	.036	.029	.345	.330	.260	.593
P. humiflora (NMP)	.019	.021	.394	.364	.203	.728
P. cryophila (NMP)	.0335	.015	.276	.343	.333	.410
P. repens (BP)	.017	.042	.123	.531	.286	.152
P. angustata (NMP?)	.049	.275	.2215	.419	.283	.326

[a] Analyses kindly provided by Prof. H. G. and I. Baker from samples supplied by the authors.

is marginal in this respect. *Protea repens,* a BP protea, has a sucrose-poor nectar ("hexose-rich") (0.152), which is confirmed by other studies (Mostert et al., 1980; Cowling, 1978). Cowling (1978), however, reported that some presumably BP proteas (*P. longifolia* Andr.) also have high sucrose concentrations. The importance of the differences in the small amounts of melzitose and maltose present in the samples is difficult to assess, although *P. angustata* has considerably higher values than the other species.

Amino acid composition. The significance of the amino acid composition of the nectar is difficult to evaluate (Table 6), but the relatively small quantitites present suggest they have no important nutritional value for small mammals. This should be expected in non-coevolved systems, where the nectar is apparently not an essential component of a pollinator's diet (see section on Reward). The amino acids may, however, impart taste to the nectar (Baker et al., 1978).

Nectar odor. The heads of all NMP proteas emit a "yeasty" or fermented odor, as previously mentioned, but two variations are apparent. *Protea amplexicaulis, P. cryophila, P. humiflora, P. recondita,* and *P. sulphurea* superimpose a sweetish scent to the basic yeasty theme, whereas *P. angustata, P. restionifolia* (Salisb. ex Knight) Rycroft, and *P. scabriuscula* Phill. produce a pungent odor reminiscent of rancid butter. Nectar freshly extracted from the heads of *P. amplexicaulis* and *P. humiflora* retains the odor, indicating that the volatile fraction occurs in the nectar itself.

The heads of *P. effusa, P. recondita,* and *P. sulphurea* maintained in water under laboratory conditions emitted perceptively stronger odors at night. A similar situation appeared to exist in both *P. amplexicaulis* and *P. humiflora* under field conditions. Although these observations are subjective, they complement the data on both flower opening and nectar secretion.

That the odor of *P. amplexicaulis* and *P. humiflora* attracts small mammals first became apparent when flowering heads were placed in the cages of captive animals while they were in their sleeping tube. Although the flowering heads were not visible from the tubes, the animals usually emerged within a few minutes, sniffed the air with upraised snouts, and then proceeded directly to the heads and began to forage.

FLORAL AND NECTAR PREDATION

The loss of reproductive potential in protea through predation was not a major consideration in this study, but several observations warrant mention. The fleshy bracts and styles of flowering heads in the species studied occasionally showed clear evidence of being chewed by small mammals, but in *P. amplexicaulis* this occurred on only about 1–2% of the heads. Thus predation by chewing is probably of little importance, especially since fertilized ovules might develop even if the styles were subsequently destroyed. Cowling (1978) presented evidence that the bracts might act as a carbohydrate sink, thus providing a possible reason for thier occasional exploitation by small mammals.

A more unusual and significant form of predation in proteas is the removal of entire flowering heads. The extent of such predation is indicated by the number of heads removed from *P. humiflora* on study stie B in 1978. Quadrat seven (10 m^2) had 307 flowering heads removed from the 45 individual plants occurring on the quadrat; quadrat ten (10 m^2) had 164 heads removed from 13 *P. humiflora* plants. Since *P. humiflora* averages 17.3 seeds per head (Table 9), about 8,148 potential seeds were lost. The num-

TABLE 6. Amino acid composition of nonflying mammal and bird pollinated protea nectar, graded on a scale of increasing concentration from 1–6.[a]

Amino Acid	*P. amplexicaulis*[b] (NMP)	*P. cryophila*[b] (NMP)	*P. angustata*[c] (NMP?)	*P. humiflora*[c] (NMP)	*P. repens*[b] (BP)
Alanine	1	2	1	1	1
Arginine	—	tr[d]	?	—	—
Asparagine	2	1	1–2	1	—
Aspartic	—	1	—	—	—
Cysteine, etc.	tr	tr	2	1	—
Glutamic	1	2	—	4	1
Glutamine	2	2	1–2	1	2
Glycine	1	3	1	2	2
Histidine	—	—	—	—	—
Isoleucine	1	1	—	2	1
Leucine	—	1	1	1(?)	—
Lysine	—	1	—	—	1
Methionine	1	2	—	2	1
Phenylalanine	—	2	1	1	—
Proline	2	1–2	2	1	2–3
Serine	1	2–3	1	1	2
Threonine	—	—	—	—	—
Tryptophan	1	2	—	—	—
Tyrosine	2	1	—	—	2
Valine	1	1	2	—	1

[a] Analyses kindly provided by Prof. H. G. and I. Baker from samples obtained by the authors.
[b] 5 = .1212 μg/μl.
[c] 6 = .2424 μg/μl.
[d] tr = trace.

ber of heads removed by predators in these quadrats was not obviously different than the number removed from others in the immediate study area, although the overall predation of entire heads was patchy.

The peduncles of heads removed through this form of predation were not obviously chewed, as might be expected from rodent activity, instead the heads appeared torn from the plants. Furthermore, the heads were often concentrated in discrete piles of up to 15, and many showed evidence of severe disturbance and damage. These observations suggested removal by an organism capable of pulling the heads from the plants. The chacma baboon (*Papio ursinus* Kerr), which occurs in the study area (pers. obs.), is the most likely predator because it forages in this manner (Roberts, 1951). Similar predation was also observed on a BP protea, *P. repens*. Since the heads are either severely disturbed or torn apart (but not eaten) it appears most likely that the predators are seeking either the sweet, copious nectar and/or the large scarab beetles (*Anisonyx ursus* F.) that occasionally occur in the heads in large numbers. Floral predation by primates is known in the Neotropics (Mori et al., 1978; Janson et al., 1981).

Nectar and pollen robbing may be a form of serious predation in both NMP and BP proteas. When the standing crop of nectar averages several milliliters, it offers an unusually rich energy resource and is heavily exploited by numerous insects. Mostert et al. (1980) found a total of 2,215 insects in 20 heads of *P. repens*. The largest percentages consisted of ants (19%), beetles (67%), and flies (12%). Whether these insects, which also occur in the NMP *P. amplexicaulis* and *P. humiflora*, contribute significantly to pollination is unknown. Bees also extract considerable nectar and pollen from the heads (Table 15), but whether this should be considered predation is difficult to assess because they probably also contribute to pollination (see sections on Nectar Consumption by Bees and Selective Exclosure Experiments).

Predation by ants should be expected in such a rich nectar source, but few ants were noticed around flowering heads of most proteas observed in this study. In *P. cryophila*, however, the heads were often heavily infested, especially at night.

Mostert et al. (1980), however, reported that nearly 20% of the insects on flowering heads of *P. repens* were ants.

Small Mammal and Abiotic Dispersal of Protea Pollen

Methods

Many of the small mammals captured in flowering stands of NMP proteas were tested for the presence of pollen on their rostra, and in some instances the feces were also examined for pollen.

The presence of pollen on the rostrum was tested by rubbing the area with gelatin blocks (several mm^2) containing basic fuchsin stain (Beattie, 1971), but neither the sampling procedure nor the size of the gelatin blocks was standardized. The gelatin block was then melted on a microscope slide and spread under a cover glass. Pollen is readily captured and stained by this method and the slides are essentially permanent. Fecal pellets were also analyzed for pollen using the same general technique. To avoid possible contamination, however, fecal samples were removed directly from the colon of sacrificed animals and partially dissolved in water to soften and spread the fecal material on the gelatin blocks.

To eliminate the remote possibility that these pollen loads originated by the chance accumulation of abiotically dispersed pollen, the following materials in dense stands of the NMP protea, *P. humiflora* (Jonasnek—site A), and a BP protea, *P. laurifolia* (below Jonasplaats), were analyzed for the presence of (presumably) wind-dispersed protea pollen: (1) rocks and leaf litter between protea plants, (2) living leaves not closer than ca. 20 cm from flowering heads, and (3) the bracts of flowering heads.

Results

Some protea pollen was found on the rostrum of all animals examined, but the amount varied widely, from only a few scattered grains to many thousands (Table 7). Of the 151 animals examined for protea pollen, only 15 samples contained less than 100 grains of protea pollen and only 9 had less than 50. The samples typically also contained a few non-protea pollen grains, but they averaged only 3.1 per sample; the highest number was 44. No average for the number of protea pollen grains was obtained because thousands of grains were present on many of the slides. The number of pollen grains on the rostrum is a function of how recently the animal foraged in relation to the number of groomings and wet-preenings. Snap-trapped animals often carried higher pollen loads than live-trapped animals; presumably the latter groom and preen while in the traps. During wet-preening, pollen should be ingested and feces did contain protea pollen, often in large numbers.

Table 7. $\bar{X}$ No. pollen grains in samples (N = 2) collected from various objects in a stand of flowering *P. humiflora.*

	Protea Pollen	Non-protea Pollen
Non-protea exposed leaf litter	6	56
Exposed rocks	2	11
P. humiflora bush[a]	33	82
P. humiflora heads[b]	492	75

[a] Samples collected from leaves <2 dm from flowering heads.

[b] Samples taken from bracts of flowering heads; pollen occurred primarily in dense clusters on the trichomes of the bracts.

Even in dense stands of protea, non-protea pollen usually predominated on the various objects examined, except on the bracts of flowering protea heads (Table 7). If protea pollen accumulated on the rostra of small mammals by chance, then the concentration should be proportional to that of non-protea background pollen which is not the case. Only visitation to flowering heads of protea can adequately explain both the size and composition of the small-mammal pollen loads.

Small mammals may also visit the flowering heads of BP proteas, e.g., *P. laurifolia*. In this species evidence of light chewing is occasionally evident on the bracts of the heads, but no indication of intensive rodent activity was observed on any BP protea. We sampled pollen on the rostra of five gerbils (*Tatera afra* Gray) and a single *Rhabdomys* trapped in a stand of *P. laurifolia* with no NMP proteas within at least 500 m. These animals all possessed low counts of protea and non-protea pollen on their rostra. Three of the animals sampled showed approximately equal numbers of protea and non-protea pollen grains, but had only a low total pollen count (<15 grains/sample). Two of the gerbils, however, showed approximately three to four

times more protea than non-protea pollen grains and also relatively larger pollen loads, although these were still small in absolute terms (13:55, 18:68). It is unlikely that the protea pollen in these two samples could have originated from sources other than direct visitation to the heads, since the stickiness of BP protea pollen is similar to that of the NMP proteas. The entire pattern of small-mammal visitation to various flowers needs further study and can be initially approached by simply measuring pollen loads.

POLLINATION ENERGETICS: *P. HUMIFLORA* AND *AETHOMYS*

METHODS

One object of the study was to determine the potential contribution of NMP protea nectar to the energy regime of the associated small-mammal community. The nectar production of *P. humiflora,* Jonasnek site B (for which the small-mammal composition and density are known), was analyzed in terms of the following parameters: (1) the potential volume and caloric content of *P. humiflora* nectar, (2) the metabolic rate of *Aethomys* as a representative small mammal, (3) the maximum amount of nectar that *Aethomys* will consume during a given period when maintained on a strict nectar diet, and (4) the density of the small-mammal community.

The caloric content of *P. humiflora* nectar was measured using an IKO Adiabatic Bomb Calorimeter. The basal metabolism of *Aethomys* was obtained by measuring O_2 consumption in a closed manometric system, corrected for temperature and atmospheric pressure. The accumulated standing crop of nectar per head (not freshly secreted nectar) was determined by shaking the droplets from the head and measuring the accumulated nectar. This procedure obviously leaves considerable nectar on the head and is thus highly conservative. Individual flowers with apparently freshly secreted nectar were utilized to determine nectar volume per flower.

The annual amount of protea nectar on the study site was calculated by determining the mean number of flowers per head, and the number of heads occurring in several randomly determined quadrats on grid B as a representative distribution for the entire grid (Table 8).

To approximate the amount of nectar *Aethomys* might ingest, a single animal was fed a strict diet of *P. humiflora* nectar (44% sucrose equivalents) from a graduated pipette and the con-

TABLE 8. Energetic relationships between *P. humiflora* and small mammals (Jonasnek sites).

$\bar{X}$ Nectar/ Fl. (μl) (N = 20)	$\bar{X}$ Standing Crop Nectar/Head (ml) (N = 11)	Nectar Cal/g	$\bar{X}$ No. Fls./Head (N = 12)	$\bar{X}$ No. Heads/ Plant (N = 19) Sites A & B	No. Protea Plants Sites A & B	$\bar{X}$ No. Heads/ Quad. Site B	No. Animals Sites A & B	$\bar{X}$ Cal/g/hr for *Aethomys* (Active & Grooming) (N = 4)
8.8	1.8	3,693	303	1977, A = 56.6 1979, B = 5.2	A = 221 B = 603	1979 = 58	1978, A = 38 B = 57 1979, B = 20	11.83

sumption recorded at 12-hour intervals (the quantities of nectar required for the experiment precluded a larger sample of animals).

RESULTS

The amount of energy in the annual nectar crop of *P. humiflora* can be roughly approximated from the data in Table 8. Multiply the amount of nectar produced per flower (8.8 μl) by the average number of flowers per head (303). Multiply this result (2.7 ml) by the number of heads per 10 m^2 quadrat (58) and multiply that sum (156.6 ml) by 25 (the total number of quadrats). Thus, roughly 3,915 ml of nectar can be expected from the *P. humiflora* plants on site B. One milliliter of nectar yields 0.31 g of solids, and one gram of solids produces 3.7 Calories. Thus the 3,915 ml of nectar on the study site yields 4,490 C. *Aethomys* requires approximately 14.1 C. per 24 hours. The 20 animals occurring on grid B in 1979 would require 282 C. per day to satisfy their basic energy requirements. If 50% of the nectar is lost to predation, sufficient nectar would remain to supply the energy requirements of the small-mammal community for 8.0 days from an approximately 45 day flowering period. Because of the many variables involved, however, this calculation provides only a crude estimate of the actual energy relationships. It does, however, indicate that only a small fraction of the annual energy needs of the small-mammal community can be met by protea nectar.

The single *Aethomys* maintained on *P. humiflora* nectar consumed an average of 6.55 ml/day, which was approximately equal to the amount of nectar taken during the first feeding bout of about 10 minutes at the initiation of the experiment (6.4 ml). Predictably, a strict diet of *P. humiflora* nectar results in progressive weight reduction (16.1% of body wt.) and death (in five days).

Seed Set in Protea

METHODS

Seed set was determined by cutting transversely through the fruiting heads at mid-ovary level with a sharp, thin blade. This is possible because the fruits (achenes) are tightly packed and remain firmly attached to the receptacle of the head for several years. Interestingly, the individual fruits remain attached to the head during this period whether or not they develop into viable seed. Furthermore, viable and sterile achenes do not obviously differ morphologically. When the heads are cut transversely at mid-ovary level, however, viable, endosperm-containing seeds are readily identifiable by their soft, milky-white texture; whereas seeds interpreted as sterile have a dull-white, dry, fibrous content (Fig. 5). Seed set in this study is thus defined as the number of achenes per head containing endosperm expressed as a percentage of the total number of flowers.

RESULTS

Seed set is generally low in both BP and NMP proteas, and in Proteaceae in general. Excluding species with small sample sizes (<10), average seed set ranges between 6 and 15%, with the exception of *P. recondita,* which developed 18 and 29% seed set from two populations (Table 9). Although the sample sizes are not large for most of the species (ca. N = 10), we found no significant variation in the 1978 seed crop for *P. humiflora* when more than 10 heads were sampled. While the annual seed set in *P. humiflora* differed significantly between 1977 and 1979 (P = .01) and between 1978 and 1979 (P = .01), the absolute change itself was not great. No significant difference was observed between seed set in 1977 and that in 1978 (P = .18), but the annual rainfall differed greatly. Although the percentage of seed set may not vary greatly from year to year, the number of heads per plant may well differ appreciably, but few data are available on this point (Table 8).

Little evidence of insect predation was noted in fruiting heads. Larval insects were infrequently observed, and were only occasionally abundant in a particular head. Such predation seems unlikely to affect the statistical data significantly.

Finally, what factors produce the typically low seed set (1–30%) in these and other proteas (Table 9)? Lack of pollination and resource availability are commonly accepted explanations for low seed set, but Casper and Wiens (1981) demonstrated that in *Cryptantha* (Boraginaceae) a significantly greater number of embryos are initiated than develop into seeds. More recent studies of *Cryptantha* (Casper, 1982) showed that embryo reduction cannot be attributed to inadequate pollination nor to resource availability, thus suggesting genetic control.

The consistently low seed set in both BP and NMP proteas, and the apparent occurrence of similarly low seed set in Australian proteaceous

TABLE 9. Seed set in nonflying mammal and bird pollinated proteas.

Species	$\overline{X}$ No. Flowers/Head	Range	$\overline{X}$ No. Seeds/ Head[a]	Range	% Seed Set	Pollination Type	Study Site
P. amplexicaulis	157 (N = 15)	136–176	11.5	0–42	7.3	NMP	Jonasplaats
P. arborea	244 (N = 2)	221–267	9.5	6–13	3.9	BP	Jonasnek
P. cryophila	1,024 (N = 12)	749–1,217	154	90–227	15.0	NMP	Sneeubergnek
P. effusa	157 (N = 10)	136–178	17.4	2–30	10.8	NMP	Murray Farm
P. humiflora	303 (N = 12)	248–373	17.3	0–95	6.0	NMP	Jonasnek
P. laurifolia	283 (N = 10)	230–346	19.4	0–55	7.0	BP	Murray Farm
P. magnifica	374 (N = 2)	349–398	5	4–6	1.3	BP	Jonasplaats
P. pendula	157 (N = 10)	136–178	17.4	2–30	11.1	NMP(?)	Murray Farm
P. punctata	138 (N = 11)	112–155	12.3	2–32	9.0	BP	Sneeubergnek
P. recondita (1)	258 (N = 10)	118–379	75.9	23–149	29.3	NMP	Sneeubergnek
P. recondita (2)	393 (N = 11)	338–436	69.6	18–148	18.1	NMP	Murray Farm
P. scolependrifolia	194 (N = 13)	160–260	16.9	0–51	9.0	NMP	Jonasplaats
P. subulifolia	105 (N = 21)	88–128	15.5	0–51	14.3	NMP	Jonasplaats
P. sulphurea	500 (N = 8)	416–588	15.3	0–53	3.0	NMP	Ouberg Pass

[a] N same as column 1 unless otherwise indicated.

genera (Rourke & Wiens, 1977; Carpenter & Recher, 1978b) also suggest that genetic factors may play a role in controlling seed set in Proteaceae, but experimental verification is needed.

GENETIC COMPATIBILITY

METHODS

Protea humiflora was tested for genetic compatibility by enclosing individual flower heads in bags of lightweight, small-mesh nylon with a basal drawstring designed to exclude potential pollinators. Exposure to wind and rain sometimes matted the nylon exclosure bag against the wiry styles, which may have exposed the stigmas to cross-pollination. In 1978 a large percentage of exclosure bags had holes chewed in them or were partially pulled from the heads (presumably by mice attempting to gain access to the highly nectarous heads). Crossing experiments with these species are difficult to implement under field conditions.

Pollen must be physically moved to the stigma to effect pollination (Fig. 4). In 1978 we attempted to cross-pollinate flowers by reciprocally exchanging pollen-laden exclosure bags between heads of different plants. Immediately after transfer the bags were manipulated to distribute pollen over the stigmas. The remaining nylon exclosures were undisturbed throughout the flowering season. In 1979, however, some heads were manipulated inside the pollen-laden exclosure bags daily for four days in an attempt to spread pollen over the stigmatic slits of newly opened flowers. The remaining heads were not manipulated. The results were analyzed statistically with the Mann-Whitney U test and χ^2.

RESULTS

In 1978 no statistical differences were observed in seed set between selfed and crossed plants ($P = .19$), but the sample size was small ($N = 6$) (Table 10). Furthermore, in 1978 both the selfed group and the outcrossed group produced significantly fewer seeds than the control group ($P \ll .01$).

In 1979 the difference in seed set between the enclosed heads which were manipulated, and

TABLE 10. Seed sets of enclosed heads of *P. humiflora* tested for genetic incompatibility.

Year	Unmanipulated Heads $\overline{X}$	Unmanipulated Heads % Control	Manipulated Heads $\overline{X}$	Manipulated Heads % Control	Artificially Outcrossed Heads	$\overline{X}$ Control
1978	4.2 (N = 6)	.23			1.2	18 (N = 103)
1979	3.4 (N = 12)	.16	2.7 (N = 9)	.13		21 (N = 35)

those which were not, was difficult to evaluate. In the non-manipulated group (N = 12) only two heads produced seed, one with 42 seeds and the other with six. In the manipulated group (N = 9), however, six heads produced seed, but none more than 10. The single head with 42 seeds in the non-manipulated group affects the statistics when using the Mann-Whitney U test. Perhaps cross-pollinating insects or some other perturbation produced this exceptionally high seed set. To avoid this problem, we compared the percentages of heads that produced any seed in the manipulated group (60%) and in the non-manipulated group (14.3%) by the McNemar variation of χ^2. This shows that the percentages are significantly different ($P \ll .01$), and suggests that self-pollination (but not necessarily autogamy) is successful to a limited extent in *P. humiflora.*

The data are difficult to evaluate because all heads placed under nylon enclosures (including those artificially crossed in 1978) typically produced significantly fewer seeds than did the control group in 1978 and 1979 ($P \ll .01$ in all cases). Thus either the enclosure treatment itself may retard seed set, or manipulation by hand does not effectively transfer pollen to the minute stigmatic slit in *P. humiflora.*

Many Proteaceae are protandrous, but this should not have affected the results since in 1979 manipulations were carried out for four days. In any case, many more of the 300 stigmas in a head should have been receptive than produced seed. Moreover, the pollen remains viable for several days (Table 11), so this should likewise not have been a problem.

To determine the breeding system in these proteas, plants should be grown under greenhouse conditions. Furthermore, a better understanding is needed as to how, when, and in what amounts pollen must be deposited on the minute stigmatic slit to effect pollination.

Pollen Viability

methods

To determine whether residual pollen (i.e., pollen retained on the rostrum following grooming) was functional, we tested *P. amplexicaulis* and *P. humiflora* pollen for length of viability. Pollen was tested for percent germination on a boron-enriched sucrose agar medium similar to that used by Taylor (1972), except that the sucrose concentration was lowered by 75%. All the pollen utilized in this study was collected from flowers that opened between 1800 and 2130 on the day the tests were initiated. A single flower of each species was removed from the original group of experimental heads and the pollen plated on agar every 12 to 24 hours for four days, and at 2130 on the sixth day following anthesis. At least two replicates were plated from each flower. Plates were maintained at ambient temperature and humidity. The percentage of pollen germinated was determined at least 16 hours after plating by counting the number of germinated and ungerminated grains visible in a single microscope field (×160) in each replicate.

results

A substantial proportion of pollen retained the ability to germinate on agar for two full days following anthesis in *P. amplexicaulis* and at least three days in *P. humiflora* (Table 11). Thus residual pollen should be capable of fertilization during this period. Some inconsistency both between replicates and for different times of plating is apparent in our results. The extremely low germination of *P. amplexicaulis* pollen on the morning of the second day, for example, is difficult to explain. Perhaps the viability of pollen from this single flower was anomalously low. Pollen plated in the evening showed a tendency to yield a higher percentage of germination than that plated in the morning, particularly in *P. humiflora.* Perhaps pollen is physiologically adapted for maximum germination under conditions to be expected at the time dispersal normally occurs.

Selective Exclosure Experiments

methods

To determine the effects of excluding small-mammal visitation on seed set in *P. amplexicaulis* (Jonasplaats) and *P. humiflora* (Jonasnek), flowering heads were enclosed in a cage of hardware cloth (mesh size 13 mm), the base of which was fitted with a nylon skirt that was tightened around the peduncle by a drawstring. The cage was supported over the inflorescence by wiring it securely to adjoining branches, thus preventing movement of the cage and possible damage to the flowers or peduncle. This cage effectively excluded all known mammals in the area (including *Mus minutoides* A. Smith, the smallest known

TABLE 11. Pollen longevity in *Protea amplexicaulis* and *P. humiflora*.

	Day No. and Observation Time										
	1		2		3		4		5		
P. amplexicaulis	0930 —	2130 (N = 3)	0930 (N = 2)	2130 (N = 3)	0930	2130 (N = 2)	0930 (N = 2)	2130 —	0930 (N = 2)	2130 —	(N = 2)
$\bar{X}$ % germination/fl.	—	.66	.01	.60	.49	.36	—	<.05	—	0	
P. humiflora	0930 —	2130 (N = 4)	0930 (N = 4)	2130 (N = 4)	0930	2130 N = 4	0930 N = 4	2130 —	0930 (N = 4)	2130 —	(N = 4)
$\bar{X}$ % germination/fl.	—	.68	.41	.74	.45	.57	—	.33	—	<.02	

TABLE 12. Seed set in protea heads caged to preclude small mammal foraging, but open for visitation by insects.

	1978					1979				
	Control		Mammal Excluded			Control		Mammal Excluded		
	$\bar{X}$	Range	$\bar{X}$	Range	Significance	$\bar{X}$	Range	$\bar{X}$	Range	Significance
P. amplexicaulis						24.04 (N = 27)	1–51	1.33 (N = 9)	0–4	P ≪ .001
P. humiflora	18.43 (N = 51)	0–95	8.73 (N = 11)	0–19	P = .06	21.23 (N = 35)	0–55	11.56 (N = 16)	1–31	P = .01

TABLE 13. Interplant distribution of fluorescing powder by (presumably) small mammals.

Protea Species	Approximate Distance from Source (m)	Points of Deposition
P. amplexicaulis[a]	1.0	Fl. head of another *P. a.*
	0.1	Runways to (but not on) fl. heads of another *P. a.*
	7.0	Runways to (but not on) another *P. a.*
	4.0	Runways to (but not on) another *P. a.*
P. humiflora[b]	3.5	Fl. head of another *P. h.*
	8.0	Runways to and on fl. head of another *P. h.*
	0.5	2 fl. heads of another *P. h.*
	2.5	2 fl. heads of another *P. h.*
P. subulifolia[a]	2.0	Runways to (but not on) another *P. s.*
	0.5	Fl. head of another *P. s.*
	1.5	Shoots (but not fl. heads) of another *P. s.*
	7.0	Runway and shoots (but not fl. head) of another *P. s.*
	0.5	Shoots and fl. heads of another *P. s.*
	0.5	Runways and shoots (but not fl. heads) of another *P. s.*
	15	Runways and fl. heads of another *P. s.*

[a] Jonasplaats study area.
[b] Jonasnek study area (site B).

rodent to occur in the study area), but allowed easy access to insects, especially honey bees. Seed set in the caged heads was compared with that of control heads, i.e., heads on the same or adjoining branches left open to natural pollination. The data were analyzed for significance utilizing the Mann-Whitney U test.

RESULTS

Excluding small mammals from the heads of NMP proteas reduces seed set by approximately 50% in *P. humiflora* (Table 12). In 1978 the differences in *P. humiflora* between the controls and the rodent-excluded heads approached significance ($P = .06$), but in 1979 the differences are considered significant ($P = .01$). We have no obvious explanation for the variable results obtained from the experimental groups between 1978 and 1979, except for the reduced sample size in 1978 ($N = 11$) and general improvement in the technique for placing exclosures over the heads in 1979.

Experiments on *P. amplexicaulis* were conducted only during 1979, and seed set in caged heads was reduced more than 95% in comparison to controls ($P \ll .01$). The sample size, however, was small ($N = 9$) and the experiments were undetertaken comparatively late in the flowering season.

FLUORESCING EXPERIMENTS

METHODS

To determine the extent of intra- and interplant movement of pollen and small mammals, the flowering heads of three species of protea (*P. amplexicaulis, P. humiflora, P. subulifolia*) were dusted with fluorescing powders (Hercules Radiant Pigment Type R 103 G) of various colors. Approximately a half teaspoon of powder (or paste produced by adding 50% ETOH) was applied over unopened florets at the center of a flowering head, avoiding the more peripheral open (and presumably nectar-containing) flowers. The heads of each plant were treated with a single color of fluorescing powder. Captive *Aethomys* foraged as readily on powdered heads as on non-powdered heads. By using the paste, which left a delicate, easily broken crust, we avoided possible contamination of adjoining plants by wind-blown powder.

Heads were normally treated at dusk to avoid possible distribution of the powder by diurnal insects. Observations of other flowering heads, or animals trapped in the area, for traces of fluorescing powder were made with a long-wave UV lamp late the same night or early the following morning before the initiation of insect movement. Observations on mice, however, were con-

TABLE 14. Small mammals captured carrying fluorescing powders applied to *P. humiflora* flowering heads (Jonasnek, site B).[a]

Animal	Approximate Distance from Source to Capture Point (m)	Portions of Animal Carrying Fluorescent Powder
Acomys	5	Hind feet, tail
Acomys	12	Rostrum, rear feet
Aethomys	9	Rostrum, front feet
Rhabdomys	3	Rostrum, chest, front feet
Rhabdomys	13	Rostrum, front feet
Rhabdomys	20	Rostrum, front feet

[a] A single *Aethomys* was captured at the *P. restionifolia* study site (Pocskraal) that bore two colors of fluorescing powders on the rostrum and front feet indicating visits to both heads approximately 15 m apart.

tinued on *P. humiflora* for three days. After the first night, only animals bearing large concentrations were recorded because many of the traps became lightly contaminated from recaptured animals carrying fluorescing powder. The high concentrations of fluorescing powder seen on some mice, however, could only have originated directly from the powdered heads.

RESULTS

Small mammals visit not only different flowering heads on the same plant, but also the heads of other protea plants for distances up to 15 m (Tables 13, 14). The large proportion of trapped animals carrying fluorescing powder on their rostra (5 or 6) provides further evidence that the small mammals foraged on these heads. In many instances the general movement patterns of the small mammals were clearly evident from the scattered fluorescing particles around the dusted heads and along the rodent runways that often interconnect NMP protea bushes.

SMALL-MAMMAL FECES IN PROTEA FLOWERING HEADS

METHODS

If small mammals regularly frequent the flowering heads of proteas, it was reasoned that they might leave behind artifacts as evidence of such visitations. The taking of nectar is difficult to detect, and the removal of pollen from newly opened flowers could occur by agents other than small mammals.

TABLE 15. Number of heads containing any fecal pellets in *P. recondita* as a function of age.[a]

Age of Heads	Fecal Pellets Present	Fecal Pellets Absent
Flowering heads fully open	6	0
Flowering heads ca. ½ open	2	4
Flowering heads <½ open	0	6

[a] While the data are highly suggestive, the sample sizes are too small to permit a χ^2 analysis for significance.

RESULTS

Small-mammal feces in the flowering heads of *P. amplexicaulis, P. cryophila, P. humiflora, P. effusa* and *P. recondita* were the only obvious artifacts discovered. Feces accumulation was found to be age dependent, the older heads containing significantly more fecal pellets than younger ones (Table 15). The presence of feces in the heads demands the presence of animals on (or above) the head at the time of defecation, and fecal accumulation within the heads indicates frequent and/or relatively long visits. In *P. recondita,* however, defecation from above is virtually impossible because this protea produces a terminal (but cryptic) head (Rourke & Wiens, 1977).

Moreover, protea pollen was present within the fecal pellets indicating that the animals made at least two visits to a flowering head: the first when the pollen that later occurred in the feces was obtained, and the second at the time of defecation.

NECTAR CONSUMPTION BY BEES

METHODS

A set of experiments was designed to determine the extent of nectar consumption in *P. humiflora* by the African honey bee (*Apis mellifera adansoni* Latreille). Two experiments compared weight losses between experimental heads (accessible to bees) versus control (inaccessible) heads. Both experiments were conducted on warm, clear, sunny days with the temperature at or above 25°C when bee activity was relatively high. Only flowering heads with at least one row of open, undisturbed flowers and observable nec-

tar were used. Heads were weighed at the beginning and end of the experiments.

In the first experiment, 20 heads were collected the afternoon of the day before the experiment and kept overnight with their peduncles in water. The next morning all heads were weighed and individually placed in a small can of water with the peduncles submerged. Ten of the containers with their single heads were placed on the ground near a flowering plant of *P. humiflora* and left uncovered (experimental group). The other ten were similarly positioned but were covered with plastic window screen (control group) to prevent insect visitation. The experiment was initiated at 1345 and terminated at 1700. Although the actual number of bee visitations to the experimental heads was not recorded, bees only rarely visited the experimental heads clustered in cans. To correct this problem the second experiment was initiated.

This experiment was similar to the first except that all heads were collected the morning of the experiment and the experimental heads (after weighing) were wired directly onto two *P. humiflora* bushes to simulate their natural distribution on the plant. Since the experimental heads could not be kept in water, the control heads were simply placed in trays under plastic screens near the bushes with the attached experimental heads. Bees appeared to visit these experimental heads just as readily as the naturally occurring heads. This experiment was initiated at 1030 and terminated at 1700. Both experiments were analyzed by the Mann-Whitney U test.

RESULTS

The difference in weight loss between the two groups in the first experiment was not significant statistically, whereas it was significant in the second experiment ($P < .01$). The average weight loss for both experimental and control heads was predictably greater in the second experiment than in the first, since heads in neither the experimental nor the control groups were kept in water (Table 16). Decrease in mean weight in the experimental group is assumed to be the result of nectar loss due to the foraging activities of bees.

Interpretation of the second experiment is complicated because the window screen covering the control group possibly reduced evaporative loss. There was little wind on the day of the experiment, however, and the experimental population was also mostly shaded by the foliage and relatively close to the ground. Thus in the second experiment we interpret possible reduction in evaporative loss produced by covering the control group with window screen as inconsequential, and assume that the differences in weight loss resulted primarily from the removal of nectar by foraging bees.

TABLE 16. Bee nectar consumption in *P. humiflora.*

Experiment	$\bar{X}$ Nectar Loss/Head (g) Resulting from Bee Foraging	S.D.	Control (g)	S.D.	Significance
1	2.04	0.63	1.75	0.86	n.s.
2	3.54	0.36	2.42	0.51	$P < 0.01$

FLOWER PREFERENCE EXPERIMENTS

METHODS

Choice tests using a T maze were conducted to determine if mice are preferentially attracted to, or preferentially forage from *P. humiflora* heads (an NMP species) rather than those of *P. repens* or *P. laurifolia* (BP species). Several species of rodents from two populations were tested: (1) individuals from the *P. humiflora* study area (*Acomys, Aethomys, Dendromus, Elephantulus*) and (2) individuals from an area at least several km away from any known NMP proteas (*Aethomys, Rhabdomys, Tatera*). The first group represented animals that were live-trapped in *P. humiflora* stands and were presumably familiar with the *P. humiflora* nectar resource ("experienced" animals), while the second group represented animals that were unlikely to have encountered *P. humiflora* or similar flowers ("naive" animals). Animals were maintained in wire cages with cardboard "sleeping tubes" prior to the experiment.

The sides and bottom of the T maze were constructed of masonite and covered above with screen mesh to permit observation. The base and arms were 38 cm long and the individual runways 10 cm wide and 15 cm high. Each end of the maze could be opened to facilitate positioning of test animals and flowering heads. Tests were conducted between approximately 2000 and 2400 hours to coincide generally with the animals' normal activity periods (Fig. 1).

TABLE 17. Flower preference of small mammals in T maze experiments.

Experimental Group	Bird Adapted Flowering Head	Nonflying Mammal Adapted Flowering Head	Significance
I. "Experienced"[a]			
Initial arm choice	17	17	n.s.
Foraging[b] choice	1	26	$P \ll .01$
II. "Naive"[c]			
Initial arm choice	17	17	n.s.
Foraging choice	0	21	$P \ll .01$

[a] Five *Aethomys* were utilized in the 34 trials.
[b] Trials resulting in no foraging were generally attributable to specific animals.
[c] Naive animals utilized in the 34 trials included: five *Tatera* (21 trials), two *Aethomys* (11), two *Rhabdomys* (2).

The experimental procedure consisted of placing a freshly picked head of *P. humiflora* in one arm of the maze and a head of either *P. repens* or *P. laurifolia* in the other arm. The position of the heads in the maze arms was determined by a coin toss. A test animal enclosed in its sleeping tube was then transferred into the base of the maze. Initial response time (time before emergence from the tube) and subsequent behavior was monitored for up to five minutes. If animals did not emerge within two minutes, the tube was tapped several times. The first direction of movement in the arms was recorded as "initial choice" (+ if toward *P. humiflora* and − if toward the alternative). The first head on which the animals foraged for ≥15 seconds was recorded as "foraging choice." If animals did not enter the maze arms, or did not forage, their responses were recorded as 0 for either initial and/or foraging choice. In both groups, initial and feeding choices were analyzed utilizing the binomial test, with H_0 that responses are random and thus should be distributed evenly between the two arms of the maze. Analysis of the experienced group excludes the single individuals of *Acomys*, *Elephantulus*, and *Dendromus* tested. Analysis of the naive group is broken into *Tatera* and all others.

RESULTS

Initial choice of maze ends was evenly distributed in both the experienced and naive animals (Table 17). In the experienced group, 17 of the 34 animals initially moved toward *P. humiflora* and the remaining 17 toward the alternative (P = .13, n.s.). In the naive group, initial choices were also split evenly, 17 to *P. humiflora* and 17 to the alternative (P = .13, n.s.).

Foraging choice, however, was not random (Table 17). Of 27 foraging responses in the experienced group, 26 were on *P. humiflora* ($P \ll .01$). Of 21 foraging responses in the naive group, all were on *P. humiflora* ($P \ll .01$). These results clearly indicate that the heads of *P. humiflora* are the preferred of the two rewards offered for both groups of animals.

The role of experience in feeding-responses was evaluated by basing expected χ^2 values on the assumption that *all* animals should forage and no animals should fail to forage. Of the 36 trials in which experienced animals initially responded, 25 foraged and 11 did not ($\chi^2 = 3.36$, n.s.), and during 38 such trials in the naive group, 21 animals foraged ($\chi^2 = 7.61$, n.s.).

DISCUSSION

SMALL MAMMAL VISITATION TO PROTEA FLOWERING HEADS

Rourke and Wiens (1977) and Wiens and Rourke (1978) presented preliminary evidence that small mammals regularly visited and pollinated the flowers of various South African proteas with which they were associated. That small mammals actually visit the flowering heads of particular proteas is supported by the following new information: (1) the presence of pollen on the rostra and in the gut of small mammals, (2) the nocturnal interfloral and interplant transfer of fluorescing powder and its occurrence on captured small mammals, and, (3) the accumulation of rodent feces in the flowering heads of various proteas.

Pollen loads. Protea pollen was found on the rostra and in the feces of all small mammals captured in association with flowering species of NMP proteas, although the amounts were highly variable (Table 1). Because protea pollen is rather sticky, it is not subject to widespread wind dispersal as demonstrated by its infrequent occurrence in background samples collected away from the flowering heads (Table 7). Table 7 also gives an approximation of the density of background pollen in the environment. The small percentage of non-protea pollen in the pollen loads carried by animals tested demonstrates that

background pollen does not accumulate in dense concentrations on the rostrum. The non-protea pollen could also originate from animals foraging on these non-protea flowers, but the low concentration argues against this, or at least suggests a considerable time lapse. If the occurrence of protea pollen on the animals were the result of chance accumulation from background pollen, then the ratios of non-protea and protea pollen on the rostrum should be approximately equal to the background samples. In fact, the ratios differ radically. Protea pollen is present in the samples taken from small mammals in concentrations averaging at least 100 grains, whereas non-protea pollen averages three grains per sample. This result is greatly underestimated for proteas because no more than 500 grains were ever counted per slide, although some slides obviously contained many thousands of protea pollen grains. The pollen in feces is almost exclusively that of protea, and is probably ingested during grooming (little pollen is apt to be ingested during nectar lapping). The data are most consistent with the explanation that the pollen on small mammals originated from frequenting the heads of flowering proteas.

Fluorescent powder experiments. The results of placing fluorescent powder on the flowering heads of several ground-flowering proteas demonstrates that interplant and interhead nocturnal distribution of fluorescing powder occurs up to 15 m from the source (Tables 13, 14). Numerous particles of fluorescing powder were repeatedly found scattered along rodent runways, strongly suggesting transport by small mammals. Nocturnal terrestrial insects would be unlikely to travel equivalent distances in the available time, nor would they be likely to follow rodent runways. Furthermore, the capture of a number of animals with relatively large amounts of fluorescing powder on their bodies, especially on the rostrum, supports their role as vectors of most of the fluorescing powder transported nocturnally.

Small-mammal feces in protea flowers. The accumulation of small-mammal feces in protea heads strongly supports the hypothesis that they regularly and frequently visit the flowering heads of NMP proteas. The presence of protea pollen in the feces provides further evidence of multiple visitation.

Exclosure experiments. Experiments designed to test for genetic compatibility inadvertently provided additional information relating to rodent visitation of *P. humiflora* heads. Twenty-four fine-mesh nylon exclosure bags were placed over heads with mature buds, but within six days 14 of the bags (58%) had holes chewed through them or were pulled partially away from the heads, or both. Placing the heads under exclosures appeared to increase the amount of nectar in the heads, thus (presumably) making them more desirable nectar sources. The only other animals in the area capable of such behavior might be chacma baboons, but this seems improbable since they were never observed near the study areas.

Although captive animals regularly foraged on NMP protea heads, no wild animals were ever observed visiting the heads. Such observations are technically difficult because the species we studied most extensively (*P. amplexicaulis, P. humiflora*) have both geoflorous and cryptic heads, and the small mammals, except *Rhabdomys,* are nocturnal. A single *Aethomys* was seen in a bush of *P. amplexicaulis* at approximately 2230 hours, but it did not visit a flowering head during the several minutes of observation. Two rodents, (*Aethomys* and *Rhabdomys*) were caught in snap traps high in the branches of *P. humiflora* near flowering heads, and many animals were captured beneath protea bushes.

DOES SMALL MAMMAL VISITATION EFFECT POLLINATION?

Several lines of evidence support the contention that small mammals visit the flowering heads of proteas. But what information indicates that these visits also result in pollination? The best evidence originates from observations of: (1) the foraging activities of captive small mammals on the flowering heads of various proteas, (2) floral morphology, and (3) selective exclosure experiments.

Nectar foraging and putative pollination by small mammals. Some individuals of each species listed in Table 1 (plus *Dendromus*) foraged on the heads of NMP proteas when in captivity. The responses of the various species and individuals, however, were not consistent. For example, *Aethomys* generally foraged readily, whereas *Rhabdomys* rarely foraged and its activities were sometimes destructive. *Elephantulus* occasionally licked the surface of the heads without actually lapping nectar from the nectar reservoirs. Nonetheless, every species in Table 1, at some time, foraged on the heads of NMP pro-

teas in a manner that should have effected pollination (the process is convincingly recorded cinematographically on 16 mm film).

One aspect of rodent visitation to flowering heads mentioned by Rourke and Wiens (1977) needs correction. They speculated that rodent visitation was largely destructive. This is clearly not the case. Except for pollen loss, there is little evidence of rodent visitation following nectar-foraging. The occasional chewing of florets and bracts that prompted the suggestion occurred on only about two percent of the heads in *P. amplexicaulis* and is unlikely to have effected pollination.

The orientation of the styles and nectar reservoirs restricts effective foraging only from the center of the head outward along the radii and ensures contact with the stigmatic surface (Figs. 3, 4). The critical stigma-nectar distance of ca. 10 mm makes inevitable the deposition of pollen in the region of the stigmatic slit during nectar lapping and guarantees the maintenance of pollen loads.

Selective exclusion experiments. When small mammals were excluded from flowering heads, seed set was reduced approximately 50% in *P. humiflora* and 95% in *P. amplexicaulis.* Thus it might be argued that insects and mammals are equally important in the pollination of *P. humiflora.* This conclusion would be premature, however, in the absence of data from the reciprocal experiment involving the exclusion of insects while permitting mammal visitation. Unfortunately, experiments along these lines were technically unsuccessful. On the bases of floral morphology, physiology, and animal foraging behavior, small mammals should be more efficient than insects in pollinating *P. amplexicaulis* and *P. humiflora.* More information is needed, however, to establish the relative pollination efficiency of insects and small mammals in this system.

The floral features characterizing NMP proteas presumably evolved in response to visitation by a variety of small mammals. However, some of these features (e.g., easily accessible, highly concentrated nectar and exposed pollen) also promote visitation by numerous insects, especially honey bees, that doubtless effect occasional pollination. Based on floral morphology, however, pollination by insects can occur only haphazardly when they forage for pollen or otherwise land on the stigma. While foraging for nectar (which they normally do), insects do not contact the stigma and pollination is impossible. Bees are possibly the most likely of insects to accomplish cross-pollination since they visit many plants, but scarab beetles might also function in this capacity (Rourke, 1972). Honey bees appeared to collect pollen from all species flowering during the period in which these studies were conducted (late winter–early spring). As Faegri and van der Pijl (1979) pointed out, "social bees . . . will visit any blossom that yields sufficient nectar." Bees and beetles may, however, regularly pollinate other proteas not closely related to the species in question, e.g., *P. odorata* Thunb. and *P. laetans* L. E. Davidson, respectively. Insects probably add to pollination success in some NMP proteas. Traits enhancing their visitation should therefore be selected for, or at least maintained at equilibrium, so long as those characteristics do not retard visitation by small mammals, which are presumably the more efficient pollinators.

Birds are rare and inconsequential visitors to the NMP proteas we studied. During a period of four years, involving over 2,000 hours of observation, one malachite sunbird was seen taking nectar from the rim of a flowering head of *P. humiflora,* but the styles were not contacted. Two Cape buntings (granivores) were captured in Sherman live traps arround *P. humiflora.* Although they carried protea pollen on their foreheads, we did not observe them on the inflorescences. On one occasion an automated camera photographed an orange-breasted sunbird at the flowering head of *P. cryophila.* This is in sharp contrast to the visitation pattern in Australia where flower birds as well as nonflying mammals are common visitors to proteas and other plants (Hopper, 1980, 1982; Turner, pers. comm.). The often cryptic flowering habits of many NMP proteas, the absence of visual cues associated with typical BP proteas, and the high sugar content of the NMP protea nectar, do not suggest that NMP protea flowers are important sources of nectar for flower birds (Pyke & Waser, 1981).

THE ATTRACTING SYSTEM

The most obvious attraction is odor, since the flowers of many NMP proteas are cryptic and pollination by small mammals is largely nocturnal. As previously mentioned, the yeastlike odor with its various modifications attracted captive animals.

The T maze experiments tested critically both olfactory response to protea heads and the ulti-

mate foraging choice. Because the proffered heads could not be seen by the captive animals, olfaction is the only stimulus to which they could have responded. The experiment, however, did not test whether the animals were initially responding to the heads of the BP protea (*P. repens* or *P. laurifolia*) or the NMP protea (*P. humiflora*). The results (Table 16) show that initial choice of maze arm was random, i.e., the experimental animals did not initially discriminate between the arm holding the NMP protea and that holding the BP protea, but did so only after receiving additional cues. Since the heads were randomly switched between the two maze arms, the runways may have become saturated with the scents of both heads, thus initially precluding selective odor cues. The heads of BP proteas have little scent discernable to humans and have no yeasty odor. While the initial response to the heads was olfactory, the ultimate foraging choice (virtually always the NMP protea) could also have involved visual cues.

The styles and inner surface of the bracts of *P. amplexicaulis, P. humiflora* and some other NMP proteas are whitish, whereas the outer surface of the bracts is often dark brown or purplish. The contrast produces a "target effect" by emphasizing the white center of the head in poor light. This is apparent to the human eye, but we have no experimental evidence regarding its apparency to animals, although differences in shades are presumably evident to most mammals. Hawkmoth-pollinated plants are typically white; even generally dark bat flowers often display some white which might act as a nectar guide. Different NMP proteas utilize different strategies to produce the effect and the subject deserves further study.

THE REWARD

Small mammals visit proteas to obtain nectar (as do myriads of insects and possibly also baboons). As indicated previously, the amount of nectar available to the small mammals is difficult to evaluate, although we estimated it would supply their energy needs for approximately eight days of their annual requirement.

The flowering period of *P. humiflora* lasts perhaps six weeks, and it is reasonable to assume that the small-mammal energy budget would be supplemented during this period by protea nectar. The NMP proteas, however, occur over only an infinitesimally small portion of the overall geographical distributions of the small mammals in question. In areas no more than several hundred meters from stands of *P. humiflora*, the small-mammal community is totally without this resource and is presumably not adversely affected.

The nectar resource from NMP proteas could, however, be more important to the total energy budget than the previous comments indicate. Some local immigration from adjoining areas could increase the density of the small-mammal population on the study areas. That this happens, is suggested by the apparently high density of small mammals on grid B (58 in 1978, 20 in 1979). While we have no comparable population density data for areas without NMP proteas, the small-mammal populations on our study sites appear generally high.

We consider the nectar resource of NMP proteas as primarily a supplement to the basic small-mammal diet (a sweet treat or junk-food trip?) rather than an important component of their annual energy budget. Such a "dessert" hypothesis is in clear contrast to coevolved systems, where nectar (and sometimes also pollen) forms the primary or exclusive component of the energy budget.

Furthermore, the flowering of most NMP proteas correlates with the reproductive period of the small mammals and the extra energy resource could be important to females during gestation and lactation, and also in juvenile survival. Blooming at this time should certainly enhance the possibility of flower visitation by small mammals, and selection could have shifted flowering by the NMP proteas into this period. Most BP proteas have peak flowering periods at other times. In unilaterally evolved flowers (see following section), the flowering periods appear to coincide with environmental factors that should maximize visitation. For example, pseudocopulatory orchids flower before the female wasps appear; and Janson et al. (1981) indicated that Neotropical Bombacaceae and Combretaceae pollinated by nonflying mammals flower during the dry season when fruits or other flowers are at seasonal lows. The nectar in this latter case could also be an important source of water for these relatively large pollinators. As Porsch (1934) pointed out, water is not always so readily available in the tropics as is generally assumed. Morcombe (1968) made the same argument for southwestern Australia. He commented that the majority of banksias flower during the height of the dry season, although George (1981) indi-

cated flowering in *Banksia* may not correspond so closely with the dry season as Morcombe suggested. If water is an important resource provided by nectar, this should be reflected in a low sugar concentration. In this connection, Schemske (1980) reported that *Combretum farinosa* Kunth (= *C. fruticosum*?), which flowers during the pronounced dry season in Guanacaste, Costa Rica, produces copious nectar and has among the lowest nectar-sugar concentrations (7.1%) of which we are aware. The water-resource argument needs further analysis as an explanation for dilute nectar concentration in unilaterally evolved plants occurring in at least seasonally arid regions (Watt et al., 1974; Pyke & Waser, 1981).

THE EVOLUTION OF NMP PROTEAS

COEVOLUTION, CO-OCCURRENCE, OR UNILATERAL EVOLUTION?

The South African NMP proteas are not coevolved (Rourke & Wiens, 1977; Wiens & Rourke, 1978). This statement often elicits questions from ecologists and evolutionary biologists, suggesting that coevolution is perhaps too deeply established as *the* raison d'être for the evolution of pollination or dispersal systems as Janzen (1980) has already suggested. Coevolution (Ehrlich & Raven, 1964) has provided a central paradigm for the study of plant-animal interactions and is an immensely useful concept. Pollination systems, however, are also commonly "unilaterally" evolved, i.e., plants that have profoundly altered floral function to attract a pollinator that itself has not become specialized to the flower. In other words, the system does not elicit "reciprocal selective responses" typical of coevolved systems, but rather "unilateral selective responses" on the part of the plant. A number of biologists have suggested that plants make initial evolutionary adjustments to animals, e.g., Grant and Grant (1965), Baker and Hurd (1968), Baker (1973) and Feinsinger (pers. comm.). Clearly, many generalist animals take nectar (or fruit) during times of seasonal abundance (Snow & Snow, 1971; Heithaus et al., 1974; Carpenter, 1978b). The concept of unilateral evolution is not meant to replace coevolution, but to complement it in the sense that it represents one end of a spectrum of biological interactions and coevolution another. Transitional situations will occur, but this is hardly uncommon in evolutionary classifications. Pollination systems involving single, coevolved pollinators are rare (e.g., *Ficus* and *Yucca*). Typically, guilds of pollinators act upon a series of sequentially flowering, coevolved plant species. The same principles that apply to nectar-foraging animals also apply to fruit- or seed-eating animals. Howe (1980) strongly questioned whether coevolution is always involved in interactions between the plant and the animals that disperse its seeds, preferring to consider the situation an example of "co-occurrence." Howe does not discuss whether the fruits he studied presumably evolved to entice various animals to eat them, or were at least preadapted to the extent that the animals readily foraged on them.

The NMP proteas are clear examples of unilateral evolution, since virtually all the basic features of the flowers appear adapted for the attraction and reward of nonflying mammals that presumably effect pollination while foraging for nectar. NMP proteas co-occur with honey bees, which also take nectar and pollen from the flowers and may occasionally effect pollination. The highly concentrated nectar, however, is the only trait held in common with bee-pollinated flowers. Conversely, good evidence exists that other proteas, e.g., *P. repens*, have coevolved with the Cape sugar bird (*Promerops cafer* L.). The latter commonly takes nectar (and insects) from the flowering heads and its breeding season is synchronized with the peak flowering activity of this protea. Even the young are partially fed on its nectar (Broekhuysen, 1959; Winterbottom, 1962; Mostert et al., 1980). In our view, all three of these mutualistic situations, i.e., coevolution, unilateral evolution, and co-occurrence describe common interactions between plant and animal species; the recognition of the latter two categories, each of which must involve tens of thousands of plant species, is overdue. While coevolution is a general concept, it was never intended by its formulators to be as all-inclusive as the current literature suggests (Raven, pers. comm.).

Of the pollination systems described by Faegri and van der Pijl (1979), wind, water, ant, and at least elements of bee, (social groups), bird, [various passerine groups, cf. Stiles (1981)], most flies, perhaps beetle systems, and all pollination involving mimicry (Wiens, 1978) are probably unilaterally evolved. Many of the plants known or thought to be pollinated by nonflying mammals are apparently unilaterally evolved (see Introduction). Coevolved guild systems probably occur in southwestern Australia, however, where some Proteaceae may be regularly pollinated by

the marsupial honey possum, *Tarsipes* (possibly also the southwestern pygmy possum, *Cercartetus concinnus* Gould), which shows clear adaptations for nectar and pollen feeding (Wiens et al., 1979; Hopper, 1980). The floral spectrum on which *Tarsipes* feeds and the degree to which it shares floral resources with birds is currently under study (Hopper, pers. comm.; Turner, pers. comm.).

The Origin of Nonflying-Mammal Pollination Systems

Rourke and Wiens (1977) suggested that at least some of the NMP proteas evolved from bird-pollinated prototypes in both Africa and Australia, as evidenced by branching patterns of the inflorescences. Many of the NMP proteas have an axillary inflorescence apparently derived by reduction from the large terminal inflorescences of the BP proteas. Fire was also a possible stimulus in the evolution of NMP proteas through the development of rhizomaty which may have promoted geoflory.

Another hypothesis for the origin of NMP proteas is suggested by this study. Virtually all NMP proteas are characterized by small, highly localized populations often associated with specific soil types. These species are typically low shrubs largely restricted to relatively high elevations in the outlying Cape mountain systems bordering the arid Karoo (Rourke, 1980). As previously stated, the Cape flora occupies an elevated and greatly dissected landscape closely associated with the Table Mountain Sandstone. Consequently, many species in this rich flora occur only as small populations in scattered, isolated habitats, as do the NMP proteas. In contrast, many of the BP proteas are large shrubs or small trees often occurring in dense populations covering many hectares. Flowering stands of these proteas apparently attract large numbers of locally migrating flower birds with which they are commonly associated.

We propose that differences in population structure may be the single most important factor regulating the evolution of pollination by nonflying mammals in *Protea*. The continuing dissection of the Table Mountain Sandstone and the progressive restriction of species having highly specialized ecological requirements (especially for soil types), may have provided nonflying mammals with several advantages over birds as pollinators. The small mammals involved are ubiquitous, non-hibernating, and non-migratory residents, and generalist feeders (Roberts, 1951). Such pollinators permit temporal partitioning of flowering times among sympatric NMP proteas, and may be more readily attracted to an ephemeral and highly restricted resource than more specialized feeders. They may also provide more reliable pollination service than insects (e.g., bees and beetles) whose activities are often restricted by the long periods of low temperatures characteristic of late winter and early spring when most NMP proteas flower. The occasional fluctuations in population size of small mammals, however, might be a disadvantage. No other flowers are known to be visited by nonflying mammals in these communities, and sympatric NMP proteas flower sequentially, thus presumably no competition exists for mammal pollinators among NMP species.

If the system were, indeed, derived from bird-pollinated species, the prototypes were presumably pre-adapted for nonflying-mammal pollinators in having (1) large heads with copious nectar secretion, and (2) an inflorescence with mechanically strengthened tissues (particularly those of the style), which could accommodate a relatively large animal without undue destruction of floral parts. Physiological and structural modifications involved in the change to the present NMP type include: (1) the shift to nocturnal anthesis and (presumably) nectar production, (2) the production of nectar with high concentrations of sucrose and other sugars, (3) reduction of the stigma-nectar distance to about 10 mm, and (4) the production of a volatile, olfactory attractant.

The hypothesis explains why pollination by nonflying mammals probably had multiple origins, since species with cryptic, terminal heads (*P. recondita*); rhizomatous stems (*P. angustata*); cryptic, geoflorous heads (*P. amplexicaulis*); and aerial, pendulous heads (*P. sulphurea*) all represent different lines of evolution in which nonflying-mammal pollination presumably evolved independently. The common denominator among these species is their occurrence in relatively small, isolated populations. The shift to the NMP type in protea shows every evidence of being a strategy superimposed on many different life forms, each of which responded in differing ways depending on the phyletic constraints within the system.

Whether the "restricted population hypothesis" is also applicable to other examples of pollination by nonflying mammals remains to be

determined. Certainly many of the cryptic and/or geoflorous species of *Dryandra* and *Banksia* in Australia occur in small, isolated populations. In Southwestern Australia, *Tarsipes* (perhaps *Cercartetus*) is highly adapted for a diet of nectar and pollen and represents a distinct line within its family. This suggests an older and long-established, flower-animal interrelationship in Australia, as Sussman and Raven (1978) and Ford et al. (1979) suggested, even though many of the cryptic, geoflorous banksias and dryandras are probably specialized within their genera.

Sussman and Raven (1978) proposed that nonflying-mammal pollination is an old phenomenon, possibly originating in the tropics. They postulated a grand scale competitive exclusion of nonflying mammals as pollinators by flower-feeding bats, which are presently unknown in the Cape region of southern Africa or in southern Australia. Less distinctive climatic gradients, however, probably existed in the early Tertiary (Sussman & Raven, 1978). Because of the low frequency of individuals of a species in tropical forests, the "restricted population hypothesis" might not be expected to apply unless (1) plants are self-compatible [an uncommon condition according to Bawa and Opler (1975] and produce sufficient flowers to induce regular visitation by nonflying mammals, or (2) the particular plant species do not occur as highly scattered individuals in tropical forests. Bats and birds solve the problem of scattered distributions by possessing flight and trap-lining capablilities, which should make them much more competitive in tropical forests than nonflying mammals.

Since the publication of Sussman and Raven's paper, three examples of pollination by nonflying mammals have been discovered in the New World tropics. Lumer (1980) reported that rodents (*Oryzomys devius* Bangs and *Peromyscus mexicanus* Saussure) pollinate *Blakea* (Melastomataceae) in a Costa Rican cloudforest. Lumer (pers. comm.) indicates that this *Blakea* often occurs as clusters of several individuals. But *Blakea* also grows in a windy, cold environment along the continental divide. Baker (pers. comm.) suggests that the harsh, windy environment may preclude effective bat visitation to such flowers. Little is known about the occurrence of flower-feeding bats in this area, but even if flower-visiting bats were present, they might well avoid the environment where these plants occur, thus providing support for Sussman and Raven's argument. *Blakea* appears to offer some evidence for both the competitive exclusion and restricted population hypotheses.

Two additional discoveries of nonflying mammal pollination are reported for the New World lowland tropical forests. Janson et al. (1981) indicated that in the Peruvian Amazon 13 species of nonflying mammals (monkeys, marsupials, procyonids) take nectar and presumably pollinate species of *Combretum* (Combretaceae), *Quararibea*, and *Ceiba* (Bombacaceae). Steiner (1981) reported that the red woolly opossum (*Caluromys derbianus* Waterhouse) visits and presumably pollinates *Mabea* (Euphorbiaceae). This opossum also visits the typically bat-pollinated flowers of *Ochroma* (Bombacaceae) and *Trichanthera* (Acanthaceae). Steiner also suggested that the common opossum (*Didelphis virginiana* Kerr) may likewise be involved in pollination.

Janson et al. (1981) observed that species of *Combretum, Quararibea,* and *Ceiba* are unilaterally adapted for pollination by various nonflying mammals, as is *Blakea* (Lumer, 1980) and probably also *Mabea* (Steiner, 1981). Whether other tropical flowers subject to nectar foraging by nonflying mammals are adapted for pollination by these animals or by bats is uncertain. Mori, Prance, and Bolten (1978) indicated that opossums, cebus, and squirrel monkeys observed on *Lecythis* flowers are feeding opportunistically, as are (presumably) marsupials on the typically bat-pollinated flowers of *Ochroma* and *Trichanthera* (Steiner, 1981). Janson et al. (1981) stated that some primate visitation is clearly opportunistic and destructive.

With respect to population structure, Steiner (1981) reported that *Mabea* may also have a clumped distribution, and suggested that such distributions may be more common in the tropics than was previously thought likely (Hubbell, 1979). Janson et al. (1981) mentioned that *Combretum* and *Quararibea* are not uncommon in the study area, but that *Ceiba* has a widely scattered distribution.

The reports of pollination of the baobab by the bush baby (Coe & Isaac, 1965) and of genets taking nectar from the flowers of *Maranthes* (Chrysobalanaceae) (Lack, 1977) in tropical Africa need further study to determine the basic pollinator adaptations of the flowers, although Lack indicated that *Maranthes* is primarily bat-pollinated. Baobabs are bat-pollinated in west Africa (Baker, 1961 and pers. comm.; Jaeger, 1954—cited by Faegri & van der Pijl, 1979).

A number of low or prostrate proteas occur in tropical Africa, e.g., *P. enervis* Wild, *P. heckmanniana* Engl., *P. paludosa* Welw., *P. secundifolia* Hauman (Beard, 1963), but the pollinators are unknown. A study of these species may well provide additional information on Sussman and Raven's competitive exclusion hypothesis as applied in the Old World tropics. Data currently emerging from the Neotropics indicate that nonflying mammals are not necessarily out-competed by bats.

Is There a Class of Flowers Adapted for Pollination by Nonflying Mammals?

The existence of a class of flowers adapted for pollination by nonflying mammals was suggested by Rourke and Wiens (1977). Their argument was based primarily on the parallel floral evolution between South African species of *Protea* and a number of Australian proteaceous, and possibly some myrtaceous genera. The problem was discussed by Sussman and Raven (1978) and by Armstrong (1979). The discovery of additional instances of nonflying-mammal pollination in the Neotropics by Lumer (1980), Janson et al. (1981), and Steiner (1981), and in Australia (Hopper, 1980, 1982; Turner, in prep.) provide additional information on the subject.

Janson et al. (1981) in their extensive studies of Amazonian nonflying-mammal pollinators provided the most important new data. They generally supported the concept of a class of flowers adapted for pollination by nonflying mammals, but stressed that sufficient attention has not been given to the possible role of bats in the pollination of the flowers on which they frequently observed nonflying mammals foraging for nectar. In tropical regions, the differential effectiveness of bats and nonflying mammals in pollinating flowers visited by both groups was discussed by Sussman and Raven (1978), but detailed analyses are needed. In Australia and south temperate Africa a similar problem exists, but it involves birds and nonflying mammals in the former, and insects and nonflying mammals in the latter. Janson et al. (1981) emphasized that many flowers growing in their study area are morphologically similar to those regularly visited and presumably pollinated by nonflying mammals, yet those flowers are ignored by these animals. Thus physiological characteristics, such as odor and nectar must share equal importance with floral structure in identifying floral classes.

Janson et al. (1981) suitably amended the list of structural features proposed by Rourke and Wiens (1977) to include characteristics of the Combretaceae and Bombacaceae they studied. Most notably, the stigma-nectar distance is increased to accomodate the larger visitors, and the flowers are short-lived. Some flowers lack an odor, but probably possess visual cues that may serve to attract the diurnal primates and procyonids that possibly lack the well-developed olfactory senses of rodents. This dichotomy of characters among nonflying mammal-pollinated flowers is not unexpected. Wiens and Rourke (1978) suggested the category might be composed of subgroups. Interestingly, Porsch (1934) originally suggested one class of flowers adapted for mammal pollination, including chiropterophily as a subgroup—a suggestion worth reconsidering. The flowers of *Blakea* (Melastomataceae) (Lumer, 1980) differ in a number of respects from those of Bombacaceae, Combretaceae, Myrtaceae, and Proteaceae, although *Mabea* (Euphorbiaceae) (Steiner, 1981) appears to have no features departing radically from those mentioned by Rourke and Wiens (1977) and Janson et al. (1981). The floral features of *Blakea* need further analysis in this regard, particularly in relation to odor and nectar characteristics. As information accumulates, more additions and modifications to the proposed syndrome will probably be necessary.

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THE MAIZE AND TEOSINTE MALE INFLORESCENCE: A NUMERICAL TAXONOMIC STUDY[1]

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ABSTRACT

The genus *Zea* consists of the world-wide cultigen, maize, and its wild and weedy relatives, the teosintes, native to Mexico, Guatemala, and Honduras. This study investigates the comparative morphology of the male inflorescence (tassel) from a large sample of teosinte populations and selected maize races. The reason for focusing on the tassel is simply that as an inedible structure it escaped the direct effects of those forces of human selection specifically aimed at its edible female counterpart, the maize ear. Thus, the tassel is the more appropriate morphological structure for comparing maize and teosinte from a taxonomic standpoint. Thirty-six populations of teosinte and four of maize were analyzed. Most of these were either collected from single localities in the field or grown from seed in a common garden near Homestead, Florida. Seventeen morphological traits of the tassel and spikelet were measured on all specimens. The measurements were subjected to canonical variate analysis, a multivariate statistical technique. Consideration of the results obtained in conjunction with cytological, biochemical, and genetic data in the literature led to the circumscription of the following taxa: I section *Luxuriantes*—(1) *Zea diploperennis*; (2) *Zea perennis*; (3) *Zea luxurians*; II section *Zea*—(4a) *Zea mays* ssp. *mays*; (4b) *Zea mays* ssp. *mexicana*; (4c) *Zea mays* ssp. *parviglumis*. The latter taxon contains vars. *parviglumis* and *huehuetenangensis* which, though morphologically similar, differ substantially by some genetic measures. Each taxon is described and illustrated with emphasis on the tassel and spikelet. The morphological data demonstrate that the annual teosintes are not intermediate between maize and *Zea diploperennis*, a fact which casts doubt on the recent hypothesis that these annuals represent the hybrid offspring of *Zea diploperennis* and a "hypothetical wild maize." Furthermore, the morphological-taxonomic evidence lends credence to the hypothesis that annual teosinte is the direct ancestor of maize; either *Zea mays* ssp. *parviglumis* or ssp. *mexicana* gave rise to cultivated maize.

The genus *Zea* consists of a small group of annual and perennial grasses including the economically important cultigen, maize (*Zea mays* ssp. *mays*), and its wild relatives, the teosintes, which are native to Mexico, Guatemala, and Honduras. There are four species included under the popular name teosinte according to the latest taxonomic treatment (Iltis & Doebley, 1980). Thus, *Zea* includes, in addition to the cultigen listed above, the following taxa: (1a) *Zea mays* ssp. *mexicana* from central and northern Mexico, including races Chalco, Central Plateau, and Nobogame of Wilkes (1967); (1b) *Z. mays* ssp. *parviglumis* var. *parviglumis* from southwestern Mexico (= race Balsas of Wilkes); (1c) *Z. mays* ssp. *parviglumis* var. *huehuetenangensis* from western Guatemala (= race Huehuetenango of Wilkes), the above three all annuals; (2) *Z. luxurians*, an annual from southeastern Guatemala and Honduras; (3) *Z. perennis*, a tetraploid perennial; and (4) *Z. diploperennis*, a diploid perennial teosinte, the latter two both highly local species from southern Jalisco, Mexico (Fig. 1). These four species are separated into sect. *Zea* containing *Z. mays* with its three subspecies, and sect. *Luxuriantes* containing *Z. luxurians*, *Z. perennis*, and *Z. diploperennis* (Doebley & Iltis, 1980).

The genus *Zea*, along with the closely related genus *Tripsacum*, which ranges from South America to temperate North America, belongs to the tribe Andropogoneae of the Panicoid subfamily of the family Gramineae. In addition to similarities in general aspect, these two genera

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FIGURE 1. Distribution of native populations of the genus *Zea* (Ex Doebley & Iltis, 1980, Fig. 29). In *Zea mays* ssp. *mexicana*, the two northern stations represent the NOBOGAME and DURANGO populations respectively, the two southern clusters CENTRAL PLATEAU (western) and CHALCO (eastern). In *Zea mays* ssp. *parviglumis*, the southern Mexican cluster represents var. *parviglumis*, and the western Guatemalan one var. *huehuetenangensis*.

share in common the highly specialized cupulate fruitcase, but differ from one another in that *Tripsacum* bears its male and female spikelets in the same inflorescence, while *Zea* has separate male and female inflorescences. Additionally, the two genera differ cytologically, *Zea* with a base chromosome number of ten (x = 10) and *Tripsacum* with eighteen (x = 18).

Some authors segregate *Zea* and *Tripsacum* along with several monoecious Asiatic genera of the Andropogoneae, in the tribe Maydeae (Hackel, 1890). However, this appears to be an unnatural group whose members as a result of convergent evolution all have male and female spikelets in separate inflorescences or separate parts of the same inflorescence (Celarier, 1957; Clayton, 1973; Smith & Lester, 1980). A system that more accurately reflects the phylogeny of these genera by placing *Zea* and *Tripsacum* in one subtribe, the Tripsacinae, and the Old World genera in another, the Coicinae, has been proposed on the basis of numerical taxonomic evidence by Clayton (1973).

Although *Zea* has long held the interest of botanists, agronomists, geneticists, cytologists, and ethnobotanists, taxonomists have until quite recently ignored *Zea* and especially the teosintes. Indeed, except for an aborted attempt by Gilly in the 1940s (cf. Iltis & Doebley, 1980), it was not until Wilkes (1967), a geneticist and ethnobotanist, undertook a study of racial diversity among the teosintes that the problem was at all addressed in a detailed manner. However, Wilkes, of necessity, largely concerned himself with determining the distribution of the teosintes, relying heavily on geography for the delimitation of his six races of annual teosinte. Although he employed genetics, physiology, and vegetative morphology to a considerable extent, he paid only scant attention to floral morphology.

As a response to the need for further taxonomic study of *Zea*, and especially of its floral morphology, Iltis (1971, 1974) initiated a study of *Zea* systematics and maize evolution at the University of Wisconsin in the late 1960s. As a result of this work, two papers (Doebley & Iltis, 1980; Iltis & Doebley, 1980) proposed the taxonomic system for *Zea* outlined above. The intent of these two papers was to present the new system of classification, discuss the evidence supporting it, and review its implications for *Zea* phylogeny, but not to discuss in detail the numerical taxonomic evidence, nor the methodologies involved. The present work concerns these aspects of the project. Building on this base, some new taxonomic conclusions are drawn and suggestions for further work proposed.

The work of Iltis and myself focuses on variation in the tassel and its spikelets. This line of investigation finds its historical roots in the work of Edgar Anderson and his associates who in a series of papers (Anderson, 1944a, 1944b, 1951, 1969; Anderson & Cutler, 1942; Anderson & Brown, 1948) called attention to the taxonomic importance of the maize tassel and the need for botanists to re-direct some of their effort away from the maize ear to the tassel. Their reasons for arguing in favor of this approach seem quite reasonable, for the tassel and especially its spikelets, are much more easily measured than their highly condensed and morphologically confusing female counterparts (Anderson, 1944b; Anderson & Cutler, 1942).

In the early 1950s, Anderson's student Reino Alava implemented the first and only taxonomic study of cultivated maize based solely on tassel and spikelet characteristics (Alava, 1952). As a result of his research, Alava identified several regional trends in maize male spikelet morphology. His work, however, had little impact on those studying maize race classification, partly because his conclusions were rather limited. What prohibited Alava from generating more far-reaching conclusions was that the only specimens available for his analyses were those preserved in the Missouri Botanical Garden herbarium. Many of these were but single specimens from one locality, and thus they were unable to provide any measure of within-population variability. In addition, these specimens were grown under widely different conditions, giving rise to much environmental variability, which obscures racial boundaries.

Despite these restrictions, Alava drew one important conclusion: "Experience with wild grasses related to maize points to the male spikelets as one of the most significant features for determining relationships of maize to its possible wild ancestors" (Alava, 1952, p. 90). Two decades later, Iltis, who had formerly taken classes with Edgar Anderson at the Missouri Botanical Garden, carried Alava's line of reasoning a step further. Iltis (1974) was apparently the first to point out that the inedible tassel was particularly well suited to the task of reconstructing the evolutionary bridge between maize and its wild ancestor, because it was less drastically altered by the effects of human selection than the edible ear. This realization, and sustained emphasis by Anderson himself on the maize tassel, led Iltis (1974) to conclude that a contribution to the highly charged controversy surrounding maize evolution could be made through a systematic study of the maize and teosinte male inflorescences. Thus, Anderson, who was above all else a powerfully influential teacher, some thirty years ago planted in the minds of his students ideas which today are still bearing fruit.

Curiously, Anderson, who provided the idea to examine the maize tassel, also provided the stimulus for the development of the statistical technique used to study this structure in the present report. This came about when, as a young man, he received a scholarship to study in England under the direction of the renowned statistician and evolutionist, Sir Ronald A. Fisher (see Anderson, 1956). At this time Anderson had an active interest in hybridization between species and developed a mathematical means to distinguish the two parental types from their hybrids. He called this technique the hybrid index, a method of great simplicity as well as practicality (Anderson, 1936). Exposed to the hybridization problem by Anderson and using Anderson's data on *Iris*, Fisher (1936) devised a much more sophisticated and at the same time far less biased method of solving this problem. This method is now known as Discriminant Analysis. Other statisticians used Fisher's idea to develop Canonical Variate Analysis, the major statistical technique used in this paper. Curiously enough, these techniques failed to impress Anderson (1944a, 1956) who completely ignored them, believing as he did that disciplined intuition was more important than high-powered mathematics for solving the puzzles of the natural world.

Thus, this imaginative Midwestern botanist, who saw with intuition and who looked to the organ which "graces" the top of the corn plant as a key to the mystery of maize, left two lega-

cies, one handed down through several generations of statisticians, the other through botanists. Now joined together, these legacies provide the foundation for the work presented here.

Materials and Methods

sampling and data organization

The basic unit of analysis for this research is the local population, here defined as a group of plants growing and presumably breeding together in an area of 2,000 square meters or less. In the case of hybrid swarms of *Zea mays* ssp. *mays* and the various taxa of teosinte, only those individuals whose male and female inflorescences showed no evidence of hybridization with maize were used. Thus, the samples are intended to represent the taxa of teosinte as they maintain themselves in the wild with little or no influence from maize.

Non-random samples of eight to twenty individuals from twelve such local populations of teosinte were studied in detail (Table 1, part A). For the most part these plants were collected within 100 meters of major or secondary highways. This does not, however, indicate disturbance in all cases. While some populations grew as weeds in corn fields, others thrived in quite wild places such as dry open savannas or rocky escarpments.

To supplement the field-collected local populations, this study includes herbarium specimens collected in the wild by various botanists at different times and in different places. These specimens were organized into six groups (Table 1, part B) each of which consists of individuals from a single political state or from the vicinity of a particular city; each such group was treated as a "local population" in the analysis. Together the field-collected local populations and field-collected herbarium specimens cover the entire known geographic range of the teosintes (Fig. 2).

All the preceding field-collected plants, having been grown in their native environments, and thus under conditions to which they are unquestionably adapted, undoubtedly represent morphologically typical specimens of the taxa to which they belong. However, environmental differences among the populations, some growing along streams in the more-or-less mesic montane forest of Jalisco and others on dry rocky escarpments in the seasonally arid Balsas river drainage, modify the phenotypes to an unknown degree. This poses a problem to the interpretation of variability among populations which is best handled by growing seeds from the populations under similar conditions in a garden. For this reason the present research includes twelve samples grown in a common garden at the Pioneer Hi-Bred International Research Station near Homestead, Florida (Table 1, part C). Each of these samples was derived from seeds collected from a single local population. The morphology of these samples indicates how differences in local environmental conditions may have affected the morphology of the field-collected plants.

Another category of population samples is that composed of specimens cultivated at various times and under various conditions. These specimens were organized into six population samples based on their region of origin (Table 1, part D). Although the environmental component of differences among them is even more complex than for the field-collected population samples, they are included in the analysis because they cover some geographic areas (e.g. Honduras) not represented by the other samples.

In order to have a sample of maize varieties with which to compare the teosintes, three so-called "primitive" maize races were grown at the Purdue University Agricultural Alumni Experimental Station in southern Florida. These include Nal-Tel, Chapalote, and Palomero Toluqueño, the seeds for which were obtained from the International Center for the Improvement of Maize and Wheat (CIMMYT) in Mexico. One other maize population sample collected in the field near Toluca, Mexico, belonging to the "Mexican Pyramidal" or "Conico" race, was studied as well (Table 1, part E).

Local populations were chosen as the basic unit of analysis because individuals within a single local population are probably phylogenetically very closely related and therefore members of the same taxon in the narrowest sense. In most situations, it is not necessary for the taxonomist to attempt to distinguish between members of one local population, but only to distinguish various local populations from one another. Populations which are very similar may be placed together in the same taxon, while those which are distinct, may, depending on the degree of difference, be placed into separate taxa.

characters analyzed

To assess the differences and similarities among the 40 populations, 17 quantitative morphological traits (variates) of the tassel and spikelet were measured. Many of these are based on characters

TABLE 1. List of populations.

A. Populations Collected in the Wild:

1. *Zea diploperennis* (DIPLOPERRENNIAL teosinte). Mexico: Jalisco: With tall grass and herbs along small streams in a region of *Pinus-Quercus-Carpinus* forest, LA VENTANA, Cerro San Miguel, Sierra de Manantlan, 7 km ENE of El Durazno, 19°31′45″N, 104°13′W, alt. ca. 2,300 m. Sept. 22, 1978. *Iltis, Guzman, Doebley & Lasseigne 450.* Sample size = 20.
2. *Zea perennis* (PERENNIAL teosinte). Mexico: Jalisco: In and along a small arroyo with *Heteropogon contortus, Chaetium bromoides,* and *Leonotis nepetifolia,* in an area of former pine-oak sacatonal grassland, 9 km WSW of Ciudad Guzman. 1.5 km ESE of LOS DEPOSITOS, 19°40′N, 103°35′W, alt. ca. 1,650 m. Sept. 24, 1978. *Iltis, Puga, Guzman, Doebley & Lasseigne 550.* Sample size = 20.
3. *Zea perennis* (PERENNIAL teosinte). Mexico: Jalisco: Along dirt roads, on edges of small maize fields, and in orchards on former *Pinus-Quercus* savanna. Ca. 14 km WSW of Ciudad Guzman, 4 km WSW of Los Depositos, 0.2 km due W of PIEDRA ANCHA, alt. 2,100–2,200 m. Oct. 1978. *R. Guzman s.n.* Sample size = 19.
4. *Zea luxurians* (GUATEMALA teosinte). Guatemala: Jutiapa: Weeds in maize field and hedgerow, 2 km N of central park in EL PROGRESO, 14°22′30″N, 89°51′30″W, alt. 1,025 m. Oct. 22, 1978. *K. Lind 419.* Sample size = 20.
5. *Zea luxurians* (GUATEMALA teosinte). Guatemala: Jutiapa: On sides and top of hot dry lava cliff formed by Pan-American Highway road cut. N-side of PAH, 1.6 km E of EL PROGRESO turn-off, 14°21′N, 89°50′W, alt. 925 m. Oct. 22, 1978. *K. Lind 420.* Sample size = 8.
6. *Zea luxurians* (GUATEMALA teosinte). Guatemala: Jutiapa: In rice and maize fields, and along hedgerows, by an old road (Camino Viejo), ca. 2 km NW of EL TABLON, 3 km ENE of Jutiapa, 14°18′15″N, 89°52′45″W, alt. ca. 1,000 m. Oct. 22, 1978. *K. Lind 421.* Sample size = 11.
7. *Zea mays* ssp. *mexicana* (CHALCO teosinte). Mexico: Mexico: Weeds in maize field, Valley of Mexico, ca. 5 km SE of CHALCO at km 46.6 on road to Amecameca, 19°12′N, 98°49′W, alt. ca. 2,300 m. Sept. 11, 1977. *Iltis & Doebley 4.* Sample size = 18.
8. *Zea mays* ssp. *mexicana* (CHALCO teosinte). Mexico: Mexico: On unplowed mound in maize field, Valley of Mexico at km 20.5 on road from LOS REYES to Texcoco. 0.8 km N of Los Reyes, 19°21′N, 98°58′W, alt. ca. 2,150 m. Sept. 12, 1977. *Iltis & Doebley 8.* Sample size = 10.
9. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU teosinte). Mexico: Guanajuato: Weeds in maize field, at km 57 on road from Morelia to Salamanca, 3 km N of URIANGATO, 20°10′N, 101°10′W, alt. ca. 1,900 m. Sept. 17, 1977. *Iltis & Doebley 96.* Sample size = 18.
10. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU teosinte). Mexico: Michoacan: In maize fields, on mostly treeless hillside, lower edge of xerophytic semi-deciduous shrubby savanna, near QUINCEO, 6 km (by air) NW of Morelia, 19°43′N, 101°14′W, alt. ca. 2,000 m. Sept. 18, 1977. *Iltis & Doebley 161.* Sample size = 10.
11. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS teosinte). Mexico: Guerrero: Weeds in maize field in region of semi-deciduous savanna of Leguminosae, *Bursera, Pseudomodingium,* and tree *Ipomoea,* at km 103 on road from Iguala to Arcelia, 11 km (by road) W of ACAPETLAHUAYA turn-off, 18°23′N. 100°07′W, alt. ca. 1,050 m. Sept. 22, 1977. *Iltis & Doebley 361.* Sample size = 16.
12. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS teosinte). Mexico: Michoacan: Very steep and ungrazed south facing rocky slope with thorny shrubs, small deciduous trees and grasses, ca. 1 km S of TZITZIO on road to Huetamo, 19°34′N, 100°55′W, alt. ca. 1,500 m. Sept. 15, 1977. *Iltis & Doebley 87.* Sample size = 20.

B. Populations of Field Collected Herbarium Specimens:

13. *Zea perennis* (PERENNIAL teosinte). Mexico: Jalisco: Among sunflowers, *Bidens* and grasses, 1 mile S of railway station of CIUDAD GUZMAN, 19°41′30″N, 103°28′40″W, alt. 1,520 m. Oct. 28, 1921. *G. N. Collins, s.n.* (US). Sample size = 3.
14. *Zea luxurians* (GUATEMALA teosinte). Guatemala: Jutiapa: Near El Progreso, *Iltis G-5* (WIS), *Wilkes 43118* (2 sheets MO, US), *43122* (F); near El Tablon, *Standley 75842, 75876* (F); near Jutiapa, *Standley 76058, 76109, 76052* (F); Chiquimula: near Ipala, *Steyermark 30287* (2 sheets F). Sample size = 11.
15. *Zea luxurians* (GUATEMALA teosinte). Mexico: Oaxaca: Near SAN AUGUSTIN, Oct. 1840. *Liebman 548* (US). Sample size = 1.
16. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU teosinte). Mexico: Durango: Near DURANGO. *E. Palmer 743* (4 sheets US, MO, WIS), *G. Collins 15* (5 sheets US, WIS). Sample size = 9.
17. *Zea mays* ssp. *mexicana* (NOBOGAME teosinte). Mexico: Chihuahua: Near NOBOGAME, *Wilkes s.n.* (2 sheets F, US), *H. S. Gentry 17973* (US). Sample size = 3.
18. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENAGO teosinte). Guatemala: Huehuete-

TABLE 1. (Continued).

nango: Near SAN ANTONIO HUISTA, *Iltis & Lind G-120* (7 sheets WIS), *Wilkes s.n.* (2 sheets WIS), *43603* (US), *McBryde 81862* (2 sheets NA, F). Sample size = 12.

C. Grown in a Common Garden at Pioneer Hi-Bred International Research Station near Homestead, Florida from October 1978 to February 1979:

19. *Zea luxurians* (GUATEMALA teosinte). Seeds from Guatemala: Jutiapa: Along hedgerow, small stream and in maize field ca. 5 km W of AGUA BLANCA, 14°29′N, 89°42′W, alt. ca. 920 m. Jan. 1, 1976. *Iltis G-38*. Cult. *Doebley 376*. Sample size = 8.
20. *Zea luxurians* (GUATEMALA teosinte). Seeds from Guatemala: Jutiapa: Along hedgerow, small stream and in maize fields 1.2 km N of EL PROGRESO on road to Jalapa, alt. 1,040–1,060 m. Dec. 1975. *Iltis G-5*. Cult. *Doebley 377*. Sample size = 8.
21. *Zea luxurians* (GUATEMALA teosinte). Seeds from Guatemala: Jutiapa: Weeds in maize fields and hedgerows on slopes above laguna, 1 km E of south entrance pass, LAGUNA RETANA, 5–7–9 km N of El Progreso, alt. 1,150 m. Dec. 29, 1975. *Iltis G-20*. Cult. *Doebley 378*. Sample size = 8.
22. *Zea luxurians* (GUATEMALA teosinte). Seeds from Guatemala: Chiquimula: Maize fields and hedgerows, 2 km N of IPALA on road to Chiquimula, 14°38′N, 89°38′W, alt. ca. 800 m. Jan. 2, 1976. *Iltis G-42*. Cult. *Doebley 379*. Sample size = 10.
23. *Zea mays* ssp. *mexicana* (CHALCO teosinte). Seeds from Mexico: Mexico: Edges of maize fields 0.5 km SE of LOS REYES on road to Amecameca, 19°20′N, 98°57′W, alt. ca. 2,225 m. Dec. 1, 1971. *Iltis & Cochrane 175*. Cult. *Doebley 374*. Sample size = 10.
24. *Zea mays* ssp. *mexicana* (CENTRAL PLATEAU teosinte). Seeds from Mexico: Michoacan: Weeds in maize field, near QUINCEO, a pueblito on the slope of Pico de Quinceo, 6 km (by air) NW of Morelia, 19°43′N, 101°14′W, alt. ca. 2,000 m. Dec. 4, 1971. *Iltis & Cochrane 276*. Cult. *Doebley 375*. Sample size = 15.
25. *Zea mays* ssp. *mexicana* (NOBOGAME teosinte). Seeds from Mexico: Chihuahua: Near NOBOGAME, obtained from *G. Beadle s.n.* Cult. *Doebley 370*. Sample size = 8.
26. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS teosinte). Seeds from Mexico: Guerrero: 4.5 km E of Mazatlan on road to EL SALADO. Nov. 1972. *Wilkes s.n.* (USDA Plant Inventory No. 181, p. 220, Accession No. 384061). Cult. *Doebley 372*. Sample size = 15.
27. *Zea mays* spp. *parviglumis* var. *parviglumis* (BALSAS teosinte). Seeds from Mexico: Michoacan: Km 127 on road from HUETAMO to Morelia, International Center for the Improvement of Maize and Wheat Accession No. 8761. Cult. *Doebley 373*. Sample size = 18.
28. *Zea mays* ssp. *parviglumis* var. *parviglumis* (BALSAS teosinte). Seeds from Mexico: Michoacan: Roadside cliffs, 1 km S of TZITZIO toward Huetamo, 19°34′N, 100°55′W, alt. ca. 1,500 m. Dec. 6, 1971, *Iltis & Cochrane 308*. Cult. *Doebley 380*. Sample size = 8.
29. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENANGO teosinte). Seeds from Guatemala: Huehuetenango: Along trail at TZISBAJ, alt. 1,510 m. Feb. 1964. *Wilkes s.n.* (USDA Plant Inventory No. 177, p. 132, Accession No. 343233). Cult. *Doebley 371*. Sample size = 16.
30. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENANGO teosinte). Seeds from Guatemala: Huehuetenango: Maize fields, ca. 1.5–2.5 km ENE of SAN ANTONIO HUISTA on road to Jacaltenango, 15°40′N, 91°45′W, alt. ca. 1,300–1,400 m. Jan. 1976. *Iltis & Lind G-120*. Cult. *Doebley 381*. Sample size = 8.

D. Populations of Herbarium Specimens Cultivated under Dissimilar Conditions:

31. *Zea perennis* (PERENNIAL teosinte). Seeds or rhizomes from Mexico: Jalisco: 1 mile S of railway station of CIUDAD GUZMAN, Oct. 28, 1921. *Collins s.n.* Cult. *Iltis & Cochrane 26376* (3 sheets WIS), *26372* (2 sheets WIS); *Iltis s.n.* (WIS); *S. Calderon s.n.* (F); *Peebles & Harrison 3527* (US); *Silveus 798* (US). Sample size = 9.
32. *Zea luxurians* (GUATEMALA teosinte). Origin of seeds uncertain (see Wilkes, 1967: 11): Cultivated at different localities throughout the world. Brazil: *Luederwaldt 22277* (US), *Reits 4744* (US), *Oliva 83* (US). Cuba: *J. G. Jack 6340* (US). Hawaii: *Hitchcock 14889* (US). Phillipines: *E. D. Merrill 11222* (US). USA: Florida: (US sheet 727070). Sample size = 7.
33. *Zea luxurians* (GUATEMALA teosinte). Honduras: Choluteca: Near SAN ANTONIO DE PADUA (Standley, 1950). *Standley 27317* (2 sheets US), *Freytag s.n.* (2 sheets MO), *Molina 5881, 5882* (US). Sample size = 6.
34. *Zea mays* ssp. *mexicana* (NOBOGAME teosinte). Seeds from Mexico: Chihuahua: Near NOBOGAME, obtained from *G. Beadle s.n.* grown at Purdue Univ. Agric. Alumni Exp. Stn., Florida City, Fla. Feb.–May 1978. Cult. *Iltis & Doebley s.n.* Sample size = 5.
35. *Zea mays* ssp. *parviglumis* var. *parviglumis* (JALISCO teosinte). Seeds from Mexico: Jalisco: LA HUER-

TABLE 1. (Continued).

TITA, Cerro La Petaca, along trail to El Durazno, 8 km (by air) ESE of Casimiro Castillo, 19°33′30″N, 104°22′30″W, Dec. 14, 1977. *Guzman s.n.* Cult. *Doebley 178.* Sample size = 6.

36. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (HUEHUETENANGO teosinte). Seeds from Guatemala: Huehuetenango: Near SAN ANTONIO HUISTA. *Anderson s.n.* (MO sheet 1168094), *Weatherwax s.n.* (MO sheet 1213458). Sample size = 2.

E. Maize Populations:

37. *Zea mays* ssp. *mays* (Race PALOMERO TOLUQUEÑO). Mexico: Mexico: International Center for the Improvement of Maize and Wheat No. BA 70-539# (Mex 5). Grown at Purdue Univ. Agric. Alumni Exp. Stn., Florida City, Fla. Feb.–May 1978. Sample size = 16.
38. *Zea mays* ssp. *mays* (Race NAL-TEL). Mexico: Campeche: International Center for the Improvement of Maize and Wheat No. tep 62A 906# (Campeche 42c). Grown at Purdue Univ. Agric. Alumni Exp. Stn., Florida City, Fla. Feb.–May 1978. Sample size = 19.
39. *Zea mays* ssp. *mays* (Race CHAPALOTE). Mexico: Sinaloa: International Center for the Improvement of Maize and Wheat No. TL 7B 5# (Sin 2). Grown at Purdue Univ. Agric. Alumni Exp. Stn., Florida City, Fla. Feb.–May 1978. Sample size = 19.
40. *Zea mays* ssp. *mays* (Race Conico). Mexico: Mexico: Depauperate plants 1–1.5 m tall. 2.5 km W of VILLA VICTORIA, 48.5 km W of Toluca on road to Morelia, 19°25′N, 100°02′W, alt. ca. 2,600 m. Sept. 28, 1978. *Iltis, Doebley & Lasseigne 760.* Sample size = 7.

studied by Alava (1952) and by Wellhausen and his associates (1952). However, since differences exist in how they were applied here and elsewhere, a discussion of each of the 17 traits is necessary.

The traits measured for this study may be divided into three categories: (1) tassel, (2) spikelet, and (3) outer glume. In order to reduce error variability when measuring these characters only pedicellate spikelets from the middle portion of the central spike (see Alava, 1952) and only tassels terminating the main culm (see Wellhausen et al., 1952) were used. However, on some herbarium specimens, one cannot determine if the tassel came from the main culm or from a lateral one, so a few tassels from lateral branches may have been inadvertently included.

A. TASSEL CHARACTERS: [With the exception of branch number these characters were all measured in millimeters (mm) and without magnification.]

1. *Branch Number.* Total number of branches *excluding the central spike.* Thus, for the tassel in Figure 3 the branch number is fourteen. No attempt was made here to distinguish between primary, secondary, and tertiary branches. Such distinctions, however, are not unimportant taxonomically. In fact, Wilkes (1967, p. 110) has noted differences in degree of tassel branching between his races of teosinte. But, as Wilkes also observed, the distinctions are often obscured by environmental variability.

The terms *primary, secondary,* and *tertiary* are used differently by Anderson (1944a, 1951) and Alava (1952) on the one hand, and Wellhausen and his associates (1952) and the successive authors of the Races of Maize series on the other. What the former authors refer to as the *primary branch* or *central spike,* the latter authors term simply the *central spike* (axis). Then, single branches departing from the central axis are called *secondary branches* by Anderson and Alava, and *primary branches* by Wellhausen. In general, Anderson and Alava always designate branches one order higher than Wellhausen. The Wellhausen system is adopted here (Fig. 3) because most researchers (Wellhausen et al., 1952; Goodman, 1967; Wilkes, 1967; Goodman & Paterniani, 1969) working with maize and teosinte have used it, and because this system has the logical advantage of considering the central spike not as a branch, but as an axis (in the same way that one would not ordinarily refer to the main stem of any plant as a branch).

2. *Central Spike Length.* Distance from the tip of the uppermost spikelet of the central spike to the point of departure of the uppermost primary tassel branch (length A–D on Fig. 3). A few authors (Wilkes, 1967; Mangelsdorf, 1974; Bird, 1978) reported that the southeastern Guatemalan teosinte (*Z. luxurians*) lacks a central spike. However, all teosintes possess a central spike, although it is generally less prominent in tassels of sect. *Luxuriantes.* Photographs of southeastern Guatemalan teosinte tassels often show the central spike, which usually projects beyond the other branches (Wilkes, 1967: plate XVII; Fig. 16, this report). The confusion surrounding this

FIGURE 2. Distribution of the populations of *Zea* sampled for this research.

matter has been discussed fully elsewhere (Doebley & Iltis, 1980).

3. *Branching Axis Length* [or *Length of Branching Space* (Wellhausen et al., 1952)]. Distance along the central axis of the inflorescence from the point of departure of the uppermost tassel branch to that of the lowermost (distance D–E on Fig. 3).

4. *Central Spike Internode Length.* Distance between eight spikelet pairs in the middle portion of the central spike (distance B–C on Fig. 3) divided by seven. This average length of the central spike's internodes is a measure of its condensation. A full description of the distribution of spikelet pairs along the central spike in maize requires a measure of how the spikelet pairs are grouped together, such as the Condensation Index applied by Anderson (1944a) to the lowest primary branch. The teosintes, however, nearly always have only one spikelet pair per node (as in branch N of Fig. 3) so Anderson's Condensation Index offers little additional information.

5. *Lateral Branch Internode Length.* Distance between six spikelet pairs in the middle portion of a major lower primary branch (distance M–L on Fig. 3) divided by five. Because the tassel branches, as opposed to the central spike, do not show the severe effects of domestication, this trait, in contrast to Central Spike Internode Length, should be useful for comparing maize and teosinte.

B. SPIKELET CHARACTERS: [Measured under a binocular dissecting microscope (15×).]

6. *Spikelet Width.* Maximum width of the fully developed spikelet just prior to anthesis, (distance A–B in Fig. 4). Since many herbarium specimens were past anthesis with shriveled spikelets, there exists considerable error variability for this trait.

7. *Pedicel Length.* Pedicel length from the rachis to the base of the spikelet (distance D–E on Fig. 4).

8. *Anther Length.* Length of the longest mature anther in the chosen spikelet. When the central spike of a herbarium specimen had long passed anthesis, an anther from a spikelet of a major lower primary branch was used.

C. OUTER GLUME CHARACTERS:

9. *Glume (Spikelet) Length.* Length from tip to base of spikelet (distance C–D on Fig. 4). Measured under a dissecting microscope (15×).

10. *Glume Width.* Maximum width of glume

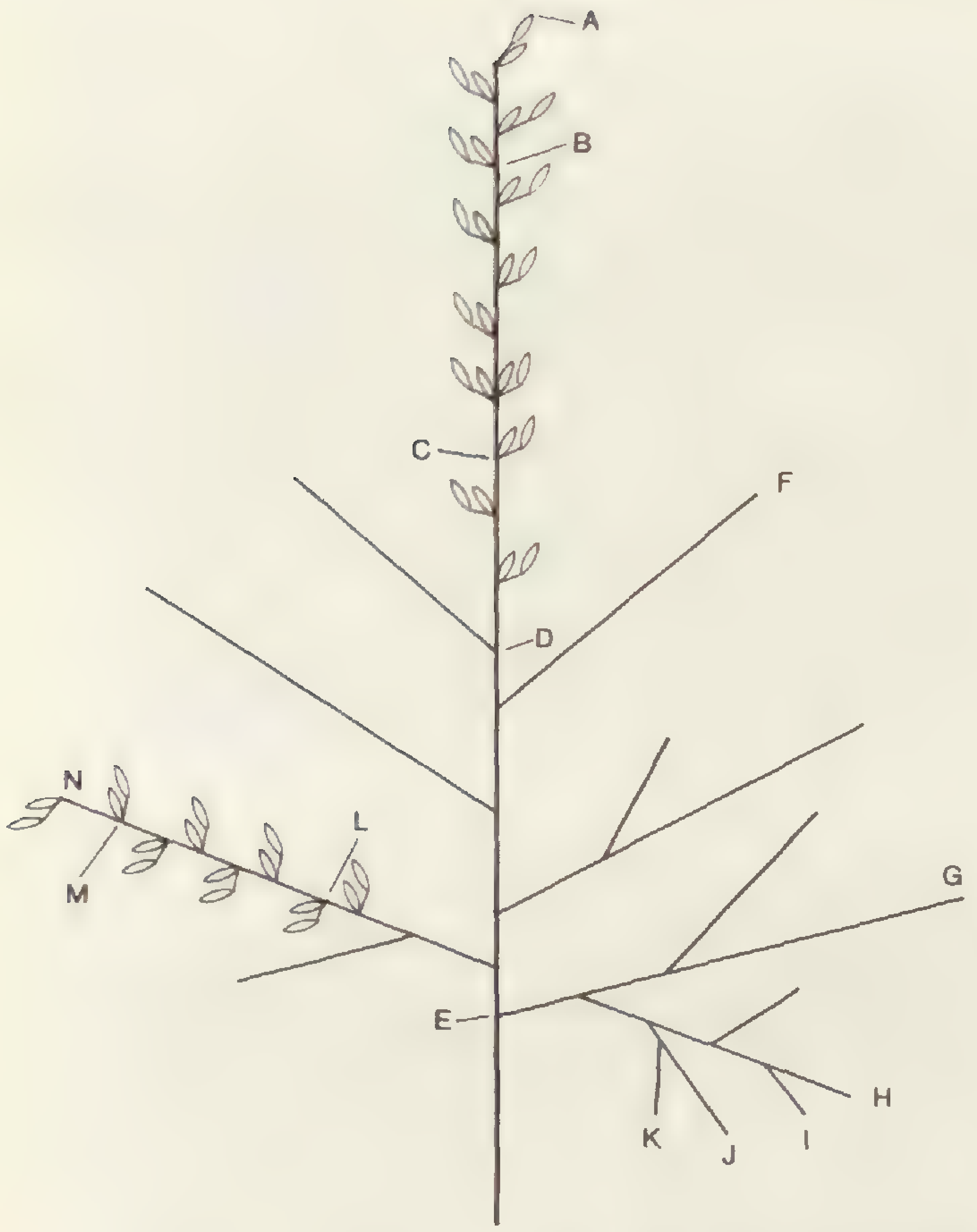


FIGURE 3. Diagramatic drawing of the *Zea* male inflorescence. F, G, and N are primary branches; H is a secondary branch; I and J are tertiary branches; and K is a quaternary branch; A–D = length of the central spike; D–E = length of the branching axis; B–C = length of seven internodes on the central spike; M–L length of five internodes on a major lower primary branch.

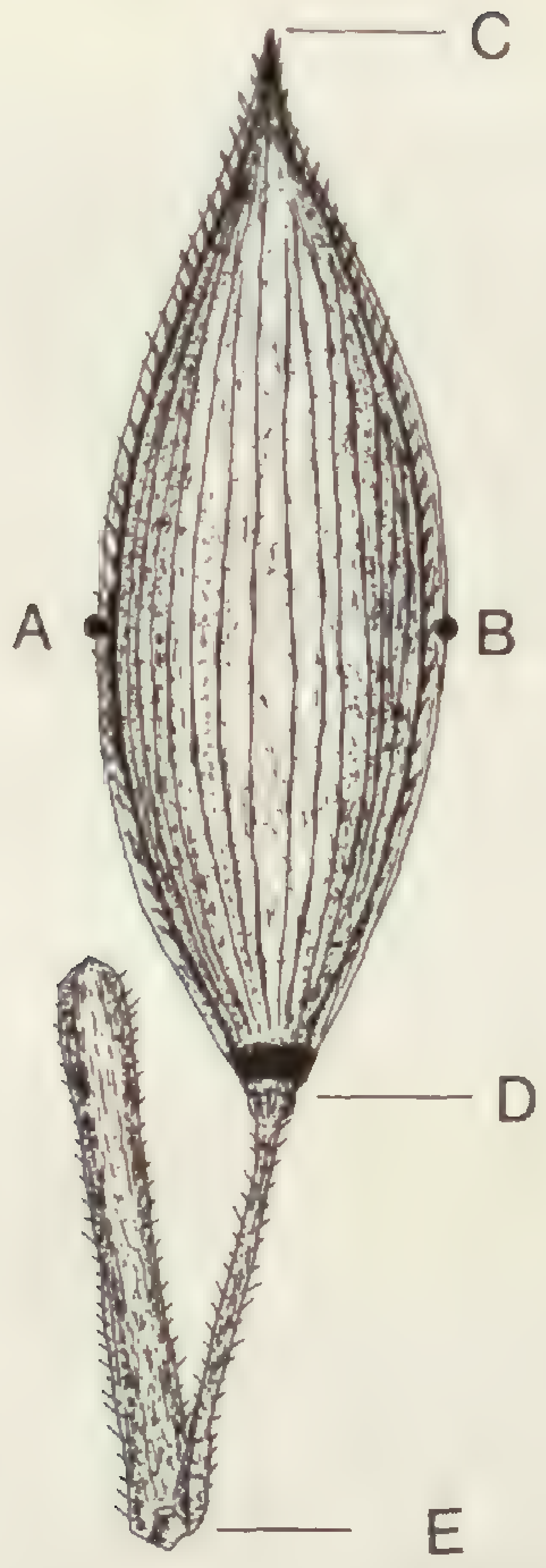


FIGURE 4. Drawing of a male pedicellate spikelet and its attached rachis internode with the sessile spikelet removed. A–B = spikelet width; C–D = glume (spikelet) length; and D–E = pedicel length.

(distance A–E on Fig. 5). The glume was removed from the spikelet, flattened, and mounted on a microscope slide in Permount, a histological mounting medium.

11. *Wing Width.* Width of wing measured where widest, usually 1 or 2 mm below spikelet tip. Wings are projections of the major lateral nerves of the outer glume and are most prominent along the upper one-third of the spikelet. Measured under a dissecting microscope (40×).

Only spikelets of the perennial teosintes possess well-developed, easily measured wings (Hitchcock, 1922; Iltis et al., 1979; Doebley & Iltis, 1980). *Zea luxurians* has much less prominent wings, while all three subspecies of *Z. mays* basically lack this structure or show only traces of it.

12. *Width of the Shoulders.* Distance between the two major lateral nerves (distance B–D on Fig. 5). Measured under a compound microscope (50×) on the same glume that was used for character 10. Although the terminology of Alava (1952) was followed here, the "shoulders" might also be referred to as the "back" of the glume. Using the term "back" would be especially appropriate for the teosintes of sect. *Luxuriantes* whose glumes are flattened on the "back," and thus lack shoulders as found in sect. *Zea.*

13. *Shoulder Vein Number.* Number of veins between the two major lateral nerves excluding the mid-vein (e.g., shoulder vein number is four in Fig. 5). Counted under a compound microscope (50×) on glumes mounted on slides.

14. *Total Vein Number.* Total number of veins including the mid-vein, shoulder veins, major lateral veins, and margin veins (e.g., total vein number is ten in Fig. 5). Counted under a compound microscope (50×) on glumes mounted on slides.

15. *Lateral Vein Width.* Width of one of the two major lateral veins. Measured with a compound microscope (50×) on glumes mounted on slides. This measurement probably contains considerable error variability because (1) the margins of the veins are often irregular; (2) many older specimens had indistinct veins; and (3) even at 50× magnification the units of measurement were too large to record this trait accurately. Nevertheless, as Alava (1952) attributed some

importance to this character, and as there are clear differences between the taxa of teosinte in this regard, lateral vein width was measured.

16. *Shoulder Vein Width.* Width of an average vein on the shoulders (Fig. 5). Measured in the same way as lateral vein width (character 15).

17. *Mid-Vein Width.* Width of the mid-vein (Fig. 5). Measured in the same way as lateral vein width (character 15). Some teosintes, and *Zea luxurians* in particular, lack a distinct mid-vein. In these cases, the vein closest to the center of the glume was measured.

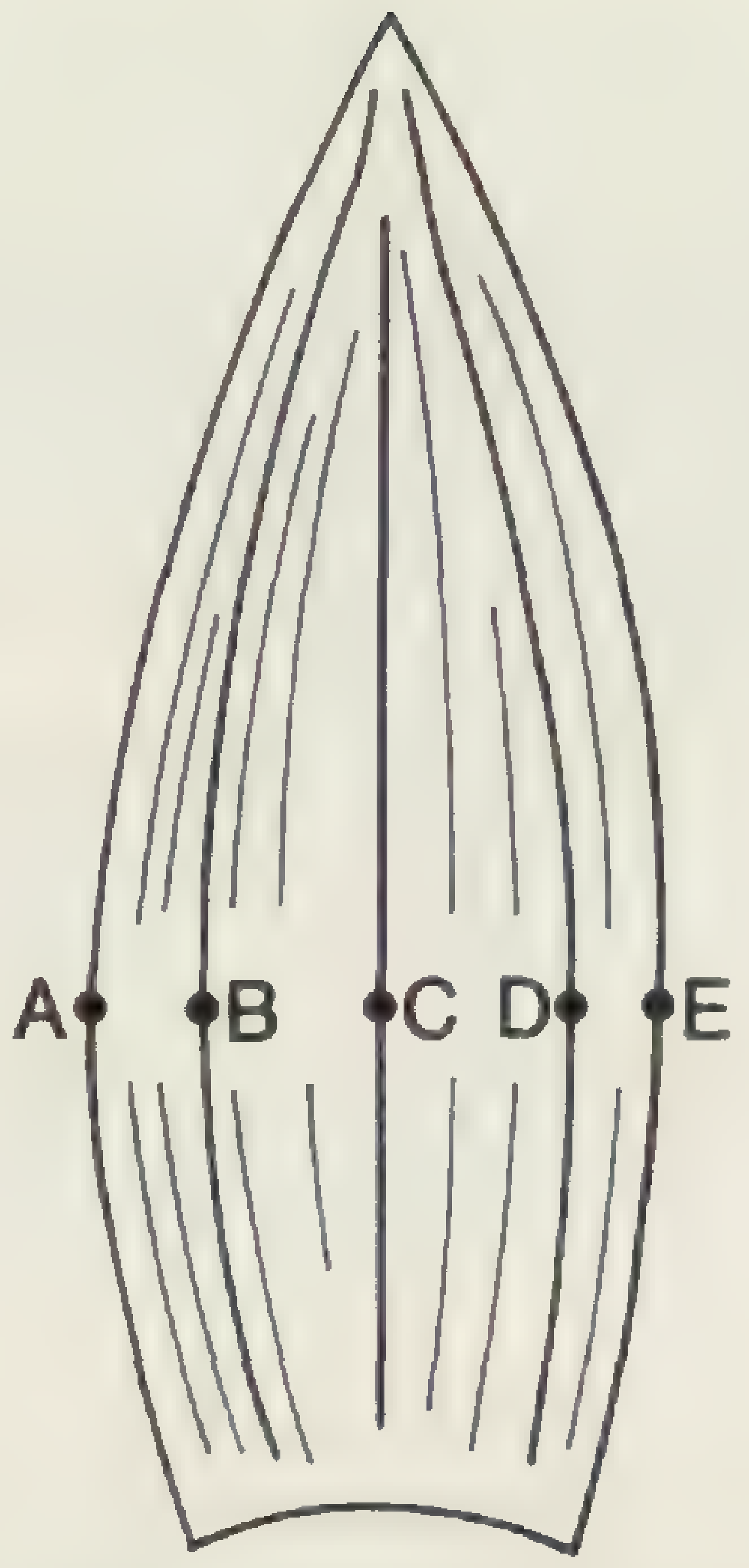


FIGURE 5. Semi-diagramatic drawing of a flattened outer glume of the *Zea* male spikelet. A and E are the edges of the glume; B and D are the lateral veins; C is the mid-vein; area A–B = left margin; area D–E = right margin; area B–C = left shoulder; area C–D = right shoulder [terminology following Alava (1952)].

DATA ANALYSIS

The quantitative morphological data were studied using canonical variate analysis, a multivariate technique, which computes synthetic variates (canonical variates) by taking various weighted sums of the original traits. The weights for the first canonical variate are calculated to give the largest possible ratio of the among-population to the within-population variance, an F-ratio. In this sense, the first canonical variate best separates all populations. Additional canonical variates are computed that, although also maximizing the F-ratio, are not correlated with previous ones, and thus contain different information (Seal, 1964; Kowal et al., 1976). One can obtain a picture of how the local populations relate to one another by graphing the first canonical variate against the second for all individuals. Graphs incorporating the third or even further canonical variates may also be useful.

Under some circumstances one wants to look only at a graph of a particular subgroup of local populations included in the overall analysis. To do so one can perform additional canonical variate analyses or close-ups including only the local populations in the subgroup of particular interest. In this way one can get a better picture of the relationships between the local populations within the subgroup. Such close-up analyses can be performed in two ways. (1) One may include all original populations in the close-up analysis but discriminate among and graph only those in the subgroup in question. Here, the pairwise distances between the populations in the full dimensional space will be the same as for the over-all analysis. However a new set of canonical variates will be computed that maximally separates only the graphed populations. This option is best when the variances and covariances of the populations in each subgroup are similar, because it uses the best estimate of the error variation. (2) However, if the variances and covariances are not similar, then including all populations would give a biased estimate of the error variation in the smaller group of populations that are being separated by the close-up analysis. Under these conditions one should exclude populations outside the subgroup in question from the close-up analysis. This will result in some changes in the between population distances. The new analysis should more accurately discriminate among the populations as error due to dissimilarity of the variances and covariances has been reduced. For the present data set, dissimilarities in the variances and covariances exist between the populations in different subgroups, so the second option was used.

The canonical variate analysis program used (CANCOV, Kowal, unpublished) standardizes the canonical variates so that the pooled within-population variance of each canonical variate equals one. When this is done each distance between a pair of populations is measured in units of the pooled within-group standard deviation (Kowal et al., 1976). This distance is referred to as Mahalanobis's distance. This is a very useful measure of distance, because if the canonical scores are approximately normally distributed, one can use properties of the normal distribution

to deduce roughly how well separated two populations are. For example, for normally distributed populations 99.7% of all individuals fall within three standard deviations (equivalent to a Mahalanobis's distance of three) of the mean. Local populations separated by twice this amount (a Mahalanobis's distance of six) will be clearly distinct from one another.

Because the distances between groups are more easily interpreted when individuals within the populations are multinormally distributed with equal variance-covariance matrices, all characters were log transformed except Shoulder Vein Number and Wing Width, which were square-root transformed. It should be realized that multinormality and equality of the variance-covariance matrices, while generally desirable, are necessary *only* if one wishes to use the technique to make statements about the probability of correctly classifying individuals. If canonical variate analysis is used solely as a method of projecting points (observations) in a multidimensional space onto a plane (a graph) as done in this paper, then normality and equality of the variance-covariance matrices are irrelevant.

Canonical analysis has three features of importance for taxonomists. First, since taxonomists tend to look for characters which show little variability within taxa and much variability between taxa, they in a sense perform implicitly in their minds what canonical analysis does explicitly, i.e., maximize the ratio of among- to within-population variance. Principal components analysis, which discriminates on the basis of variability among individuals, does not generally work as well with taxonomic problems in which the major goal is seeing how well the taxa are separated (Kowal, pers. comm.; Steudel, 1978). Secondly, canonical analysis does not require the systematist to assign local populations to any taxon, and thus allows all local populations to be judged independently of the researcher's bias as to where they belong in the taxonomic hierarchy. Finally, since canonical analysis provides a graph on which each specimen is represented by a separate point, it allows the taxonomist to keep track of individual plants. For these reasons, canonical analysis is well adapted to systematic endeavors. Indeed, it has been fairly extensively applied by both plant and animal taxonomists (Oxnard, 1969; Robinson & Steudel, 1973; Kallunki, 1976; Riggins et al., 1977; Keller, 1979; Kowal & Ruffin, 1979; Price, 1980; Doebley & Iltis, 1980; Bell & Lester, 1980; Bowman, 1980; Reynolds & Crawford, 1980).

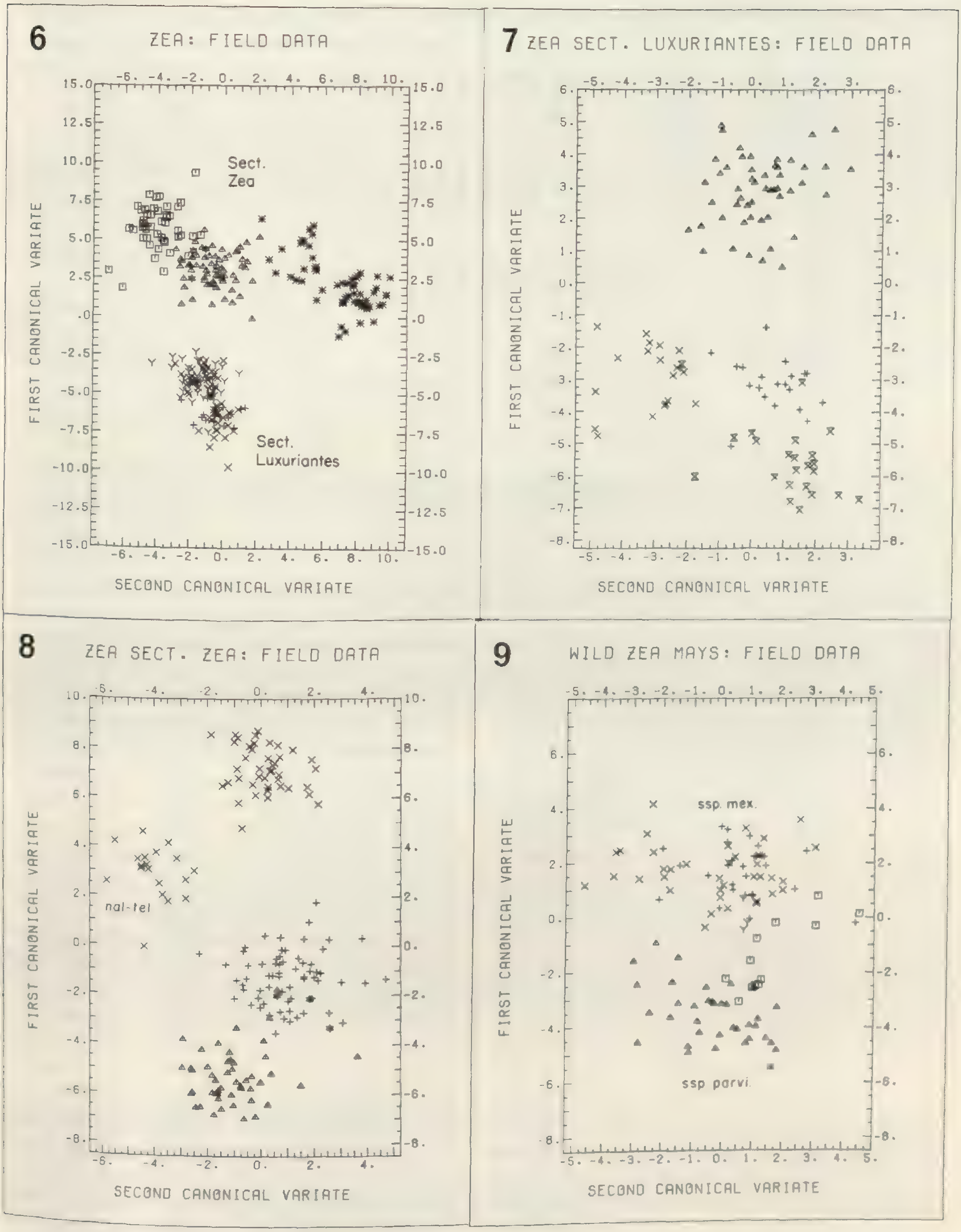
RESULTS

FIELD DATA

A graph of the first and second variates from an initial canonical variate analysis of the 18 field and four maize populations (Fig. 6) reveals two clusters: one corresponding to sect. *Luxuriantes*, which contains *Zea diploperennis*, *Z. perennis*, and *Z. luxurians*; and one corresponding to sect. *Zea*, which contains all three subspecies of *Z. mays*. The coefficients of the eigenvectors measure the contribution of each trait to each canonical variate, and each eigenvalue, expressed as a percentage of the sum of all eigenvalues, measures the relative amount of the total among-population variance explained by a canonical variate (Table 2). Each eigenvector gives the weights (in standardized form) used to calculate the weighted sum of the original traits, that is the canonical score, for an individual. From the eigenvectors, one can see that individuals on Figure 6 with long lateral branch internodes, narrow glumal wings, wide mid-veins, short glumes, and a small total vein number receive the largest values for canonical variate one. These traits best separate the two sections of the genus. Doebley and Iltis (1980) discuss additional characters useful in differentiating the two sections.

The second canonical variate on Figure 6 separates the three subspecies of *Zea mays* and shows *Z. mays* ssp. *mays* to be closest morphologically to *Z. mays* ssp. *mexicana*. For this canonical variate, the eigenvector (Table 2) indicates that individuals, like those of the maize races involved, with short central branch internodes, long glumes, few tassel branches, and a long central spike receive the largest scores. *Zea mays* ssp. *parviglumis*, on the other hand, with small glumes, long internodes on the central spike, many tassel branches, and a short central spike, receives the smallest values.

The three species that compose the lower cluster of individuals (sect. *Luxuriantes*) do not separate from one another along either axis, although the Mahalanobis's distances between these species are large (Table 3). In fact, *Zea luxurians* is very well separated from the perennial taxa ($\bar{D} = 6.1$). The explanation for this distortion is simply that because Figure 6 is in reality a 17 dimensional figure compressed into two dimen-



FIGURES 6–9. Graphs of the first and second variates from canonical analyses.—6. 18 field populations of teosinte and 4 maize populations including *Zea diploperennis* (+); *Z. perennis* (X); *Z. luxurians* (Y); and *Z. mays* ssp. *mays* (*), ssp. *parviglumis* (□) and ssp. *mexicana* (△).—7. 9 field populations of *Zea* sect. *Luxuriantes* including *Z. diploperennis* (+); *Z. perennis* from CIUDAD GUZMAN (X̄), LOS DEPOSITOS (X̄), and PIEDRA ANCHA (X); and *Z. luxurians* (△).—8. 13 field populations of *Zea* sect. *Zea* including *Z. mays* ssp. *mays* (X), ssp. *parviglumis* (△), and ssp. *mexicana* (+), and race Nobogame (★) of *Z. mays* ssp. *mexicana*.—9. 9 field populations of the wild taxa of *Zea mays* including *Z. mays* ssp. *mexicana* races Chalco (+), Central Plateau (X) and Nobogame (Y); and *Z. mays* ssp. *parviglumis* vars. *parviglumis* (△) and *huehuetenangensis* (□).

Table 2. Eigenvectors (standardized such that the largest element in absolute value equals one) and percent variance for the canonical variates from Figures 6 to 13.

Figure	6		7		8		9		10		11	
Canonical Variate	1	2	1	2	1	2	1	2	1	2	1	2
Characters												
1. BRAN-#	.015	−.500	.068	.115	−.411	−.756	−.176	−.751	−.437	.799	−.707	−.439
2. CNSP-L	.514	.459	.184	.802	.375	−1.000	−.212	−.378	−.736	.487	−.820	−.357
3. BRAX-L	.246	.120	.266	.134	−.020	−.101	.145	.371	−.350	.528	−.133	−.320
4. CSIN-L	−.089	−1.000	.080	.027	−1.000	.727	−.272	.054	−.514	.468	−.479	−.809
5. LBIN-L	1.000	.222	.404	−1.000	−.145	−.286	−.372	−.218	−.046	−.135	.056	−.281
6. SPIK-W	−.262	.233	−.178	.134	.399	−.116	.112	−.064	.259	−.251	.261	−.045
7. PEDI-L	−.062	−.335	.115	−.038	−.210	.342	.105	.168	.174	.030	.188	−.775
8. ANTH-L	.065	.209	.027	.126	−.115	.341	−.119	.013	.068	−.109	−.094	−.418
9. GLUM-L	−.766	.673	−.400	.215	.952	.597	1.000	.011	1.000	−1.000	1.000	1.000
10. GLUM-W	.094	.332	−.365	.241	.285	.197	.132	.894	.222	−.265	.189	−.614
11. WING-W	−.964	−.346	−1.000	.282	−.185	.259	−.065	−.210	.540	.092	.251	.016
12. SHLD-W	−.341	−.275	.058	−.827	−.193	.396	.144	−.956	.207	−.051	.361	.024
13. SHD-V#	−.238	−.172	.865	.079	.041	−.219	.074	.665	.736	.510	.050	−.264
14. TOT-V#	−.705	−.021	.160	.962	.095	.091	.200	−1.000	.054	.600	−.024	−.878
15. LATV-W	−.422	−.098	−.110	.751	.109	.004	.190	.404	.236	.454	.099	−.007
16. SHVN-W	.097	.025	.099	−.587	.039	−.086	−.078	−.292	−.331	−.215	−.121	−.115
17. MIDV-W	.801	.066	.153	−.452	−.259	.038	−.240	.820	−.252	−.277	−.211	−.127
Percent variance	46.26	33.10	66.81	12.65	72.93	9.21	52.08	16.34	71.97	10.70	60.72	17.46

TABLE 3. Mahalanobis's distances among populations graphed on Figure 6. Data given below are the means (and ranges) for pairwise interpopulation distances, grouped by taxa.

Species	*Zea diploperennis*	*Zea perennis*	*Zea luxurians*	*Zea mays* ssp. *mays*	*Zea mays* ssp. *mexicana*	*Zea mays* ssp. *parviglumis*
Number of populations	1	3	5	4	6	3
Zea diploperennis	—					
Zea perennis	3.9 (3.5–4.1)	4.2				
Zea luxurians	5.9 (4.6–7.9)	6.3 (5.1–8.6)	3.9			
Zea mays ssp. *mays*	11.9 (11.5–12.2)	12.0 (11.1–13.0)	12.0 (9.4–13.9)	5.6		
Zea mays ssp. *mexicana*	9.9 (8.7–10.7)	9.4 (6.3–10.2)	9.0 (7.0–12.3)	9.3 (7.0–11.3)	4.1	
Zea mays ssp. *parviglumis*	12.7 (11.6–13.6)	12.0 (9.4–14.4)	11.3 (9.4–13.9)	12.4 (9.6–14.4)	6.1 (4.5–7.3)	4.1

sions, some pairwise distances between the populations and especially between those populations within the same cluster are not accurately represented. One may obtain a better view of how the taxa within the two sections relate to one another by performing close-up analyses of each cluster as discussed in the Materials and Methods.

Figure 7 is a plot of the first two variates from a close-up analysis of the subgroup corresponding to sect. *Luxuriantes*. On this graph the five populations of *Zea luxurians*, all represented by triangles, receive positive values for the first canonical variate while both perennial species have negative scores for this variate. The eigenvector corresponding to this variate (Table 2) shows it to be composed largely of wing width and shoulder vein number, the traits that best distinguish the narrow-winged, highly-veined *Zea luxurians* from the broad-winged, fewer-veined perennials. The second canonical variate discriminates among the four perennial populations, but fails to clearly separate *Z. perennis* from *Z. diploperennis*. This is not particularly surprising as these two species are very closely related, *Z. perennis* presumably being the autotetraploid derivative of *Z. diploperennis*. The characters that best distinguish these two taxa are their rhizomes (the diploid having shorter rhizome internodes and tuber-like short shoots) and general robustness of the plants (the diploid having wider leaves and taller stems) (Iltis et al., 1979). In inflorescence morphology, *Z. diploperennis* has on the average a greater number of tassel branches and wider spikelets with wider shoulders. However, these differences are not large enough to allow its separation from *Z. perennis* on Figure 7. The basic inflorescence structure of the two taxa being nearly identical, one might treat them as two subspecies of *Z. perennis*. However, the great dissimilarities in their rhizomes and general aspect justify maintaining them as separate species (Iltis et al., 1979).

A canonical graph of the taxa of sect. *Zea* shows the maize populations separating well from the two wild subspecies of *Zea mays*, but these two wild taxa overlap somewhat with one another (Fig. 8). Of the two wild subspecies, *Z. mays* ssp. *mexicana* is closest to the cultigen maize, and closest to the Nal-Tel race of maize, in particular (Table 4). The Nobogame specimens, which have slightly smaller spikelets than the Chalco and Central Plateau races, still appear closest to *Z. mays* ssp. *mexicana* rather than *Z. mays* ssp. *parviglumis* (Fig. 8). Part of the reason for this is that, like *Z. mays* ssp. *mexicana* and unlike *Z. mays* ssp. *parviglumis*, race Nobogame characteristically has few tassel branches.

Maize separates from the teosintes along the first canonical variate primarily on the basis of its shorter central spike internodes and longer glumes (Table 2; Fig. 8). These two traits, which are correlated with the number of kernels per ear and kernel size, respectively, probably reflect the indirect effects of domestication. As the pre-Co-

TABLE 4. Mahalanobis's distances among populations graphed on Figure 8. Data given below are the means (and ranges) for pairwise interpopulation distances, grouped by taxa.

Taxa	*Zea mays* ssp. *mays*[1]	Race Nal-Tel	*Zea mays* ssp. *mexicana*	*Zea mays* ssp. *parviglumis*
Number of populations	3	1	6	3
Zea mays ssp. *mays*[1]	3.88			
Race Nal-Tel	6.7 (6.0–7.3)	—		
Zea mays ssp. *mexicana*	9.3 (8.6–10.9)	7.3 (6.4–8.5)	3.8	
Zea mays ssp. *parviglumis*	12.8 (11.8–13.9)	9.3 (8.9–9.8)	5.7 (4.4–7.0)	4.0

[1] Excluding race Nal-Tel.

lumbian Mexican Indians selected for larger grains and more grains per ear, they would have inadvertently brought about an increase in male spikelet size and a reduction in the length of internodes on the central spike (Iltis, 1971, 1981; Galinat, 1971; Beadle, 1972; Doebley & Iltis, 1980). Thus, maize differs from the annual teosintes of Mexico and west-central Guatemala mainly in characters that were transformed by human selective pressures, supporting the hypothesis that maize is domesticated teosinte.

Pinpointing the particular taxon of teosinte which was transformed into maize is more difficult. To approach this problem, one may use morphological distance (here measured with Mahalanobis's distance) to measure evolutionary divergence. This procedure is reasonable though certainly not foolproof. On this basis the teosintes of sect. *Luxuriantes,* all of which are morphologically quite distant from maize (Fig. 6; Table 3) cannot be considered likely candidates for the direct ancestor of maize (Doebley & Iltis, 1980). Of the two remaining taxa, *Z. mays* ssp. *mexicana* and ssp. *parviglumis,* the former is morphologically closest to the Mexican maize races studied here (Fig. 6; Table 3). This closeness reflects the facts that *Z. mays* ssp. *mexicana,* like these Mexican races of maize, has larger spikelets, fewer tassel branches, and a longer central spike than *Z. mays* ssp. *parviglumis.*

In Figure 8, race Nal-Tel of maize separates out from the other three maize races (Conico, Palomero Toluqueño, and Chapalote). This is of interest because races Nal-Tel and Chapalote have generally been regarded as closely related (Wellhausen et al., 1952, p. 58; cf. Goodman 1972, p. 179). Yet, the great dissimilarities between these two races in tassel and male spikelet characters mandates that we consider the possibility that their similarity in ear traits results, at least in part, from convergent evolution. The fact that the two races are so widely separated geographically—Nal-Tel from the Yucatan and Chapalote from northwest Mexico—supports this hypothesis.

Results from the study of this small sample of maize races points to the potential of tassel and spikelet traits in helping to understand the taxonomy and evolution of maize races. Such an approach certainly offers an effective and in some ways more objective means of measuring the degree of similarity of maize races to teosinte than is possible with ear characters, given the tremendous differences between the female inflorescences of these two taxa (Anderson, 1944a, 1951).

Figure 9 shows in greater detail the relationship between *Zea mays* ssp. *mexicana* and ssp. *parviglumis,* with each of Wilkes's (1967) races given a separate symbol. Again, the two subspecies separate fairly well with a small area of overlap. Similar results are obtained by graphing these populations using spikelet length versus spikelet width as done by Iltis and Doebley (1980).

Figure 9 also reveals that within *Z. mays* ssp. *mexicana,* races Chalco and Central Plateau do not separate at all, demonstrating that there is no male inflorescence morphological basis for considering them separate taxa. Within *Z. mays* ssp. *parviglumis,* vars. *parviglumis* and *huehuetenangensis* do diverge to some degree along canonical variate two, but with so few specimens

of the latter the case for granting the two races, Balsas and Huehuetenango, even varietal status is weak.

GARDEN DATA

To supplement the field data and help elucidate the degree to which environmental differences influence the morphology of the taxa, plants grown in a common garden were studied. Unfortunately, the perennials grew very poorly in the garden and often failed to produce tassels. For this reason only the annual teosintes are included here.

An initial canonical variate analysis of all 12 garden populations (Fig. 10) shows the same basic pattern as the field data. Namely, *Zea luxurians* is very distinct from the other annuals, which in turn separate into *Z. mays* subspecies *mexicana* and *parviglumis*. The major characters involved in separating *Z. luxurians* from *Z. mays* along both the first and second canonical variates are glume length, shoulder vein number, total vein number, wing width, central spike length, branching axis length, lateral vein width, branch number, and length of internodes on the central spike (Table 2). This corresponds well with the field data, which showed *Z. luxurians* to be distinct on the basis of its higher vein number, wider wings, shorter branching axis, and broader lateral nerves.

One difference between the garden and field populations is that the garden populations of the two wild subspecies of *Zea mays* separate much more effectively than the field populations, and without any overlap. The distance between these two subspecies is greater for the garden data (Tables 3 and 5). This sharpening of the differences between the subspecies probably reflects a lessening of environmental variability among local populations. The two subspecies are represented by nearly the same number of samples for the field and garden data, so the sharpening of differences probably does not reflect dissimilar sampling.

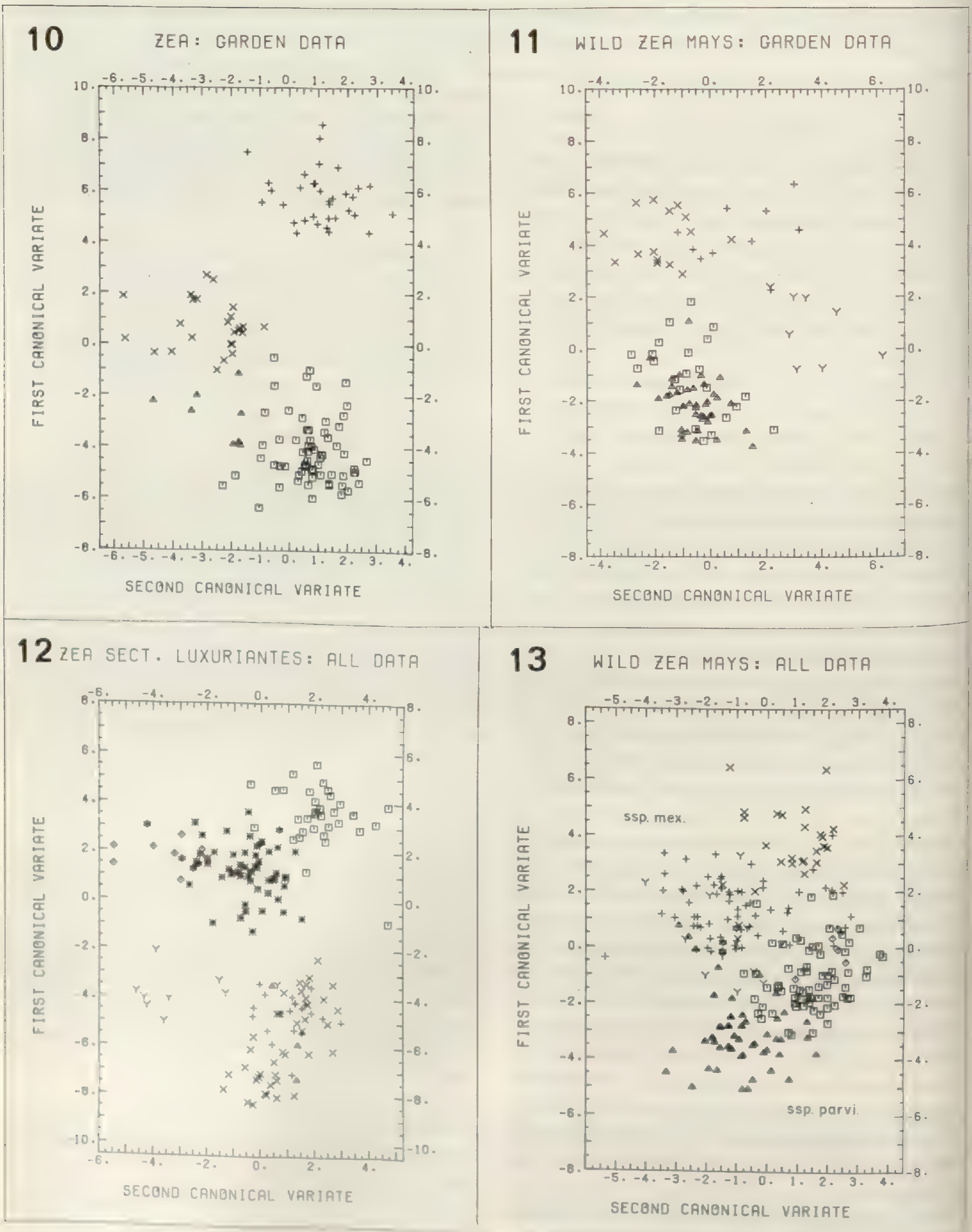
Looking more closely at the two wild subspecies of *Zea mays* (Fig. 11), one observes the same basic pattern of variation as seen in the field data except with more effective separation of the two subspecies. One other difference, as compared to the field data, is that race Nobogame appears rather distinct from the other two races of *Z. mays* ssp. *mexicana* and shows a closer association to *Z. mays* ssp. *parviglumis* (Table 5). The eigenvectors involved in Figure 11 (Table 2) indicate that while races Chalco and Central Plateau differ from *Zea mays* ssp. *parviglumis* by their longer spikelets, shorter branching axes, and fewer branches, race Nobogame is distinguished from *Z. mays* ssp. *parviglumis* by a combination of these characters, as well as fewer nerves on its outer glume and shorter internodes on the central spike.

The distinctiveness of race Nobogame for the garden data does not agree well with the field data, which showed complete overlap of this race with races Chalco and Central Plateau. The probable reason for this is that race Nobogame, being the northernmost teosinte and adapted to flower with longer days, is forced to flower prematurely in Florida before it attains much vegetative development. Thus, the plants are much more depauperate and distinct from specimens of races Chalco and Central Plateau, which flower much later in the garden and obtain a normal amount of vegetative development. For this reason, and because herbarium specimens of races Chalco, Central Plateau, and Nobogame cannot for the most part be told apart, it seems best to include these three races within a single subspecies.

MISCELLANEOUS POPULATIONS

Six populations of plants cultivated under nonuniform (uncontrolled) conditions are of interest as some of them are from areas not otherwise sampled, such as Honduras. Figure 12 includes three such populations, as well as all other populations of sect. *Luxuriantes*. On this graph the Honduras population clusters with the other populations of *Zea luxurians* as does the strictly artificial population composed of Guatemala teosinte plants (diamonds of Fig. 12) cultivated at different localities around the world. Clearly, while the Honduras population does belong in *Zea luxurians* (Guatemala teosinte), where it was placed by Wilkes (1967), more and better material is necessary to determine if it deserves distinction at the subspecific level.

Another pattern of interest revealed in Figure 12 is that the garden populations group together, as do the field populations and the uncontrolled cultivation populations. This demonstrates the extreme effects of the environment on the morphology of the plants, emphasizing the importance of comparing only plants grown under the same conditions, especially when looking at differences at the subspecific level.



FIGURES 10–13. Graphs of the first and second variates from canonical analyses.—10. 12 garden populations of teosinte including *Z. luxurians* (+); *Z. mays* ssp. *mexicana* (X), and ssp. *parviglumis* (□), and race Nobogame (△) of *Z. mays* ssp. *mexicana*.—11. 8 garden populations of the wild taxa of *Zea mays* including *Z. mays* ssp. *mexicana* races Chalco (+), Central Plateau (X) and Nobogame (Y); and *Z. mays* ssp. *parviglumis* vars. *parviglumis* (△), and *huehuetenangensis* (□).—12. 9 field, 4 controlled garden and 3 uncontrolled garden populations of *Zea* sect. *Luxuriantes* including *Z. diploperennis* (+); *Z. perennis*, 2 field populations (X), uncontrolled garden population derived from Collins's CIUDAD GUZMAN collection (Y) and Collins's CIUDAD GUZMAN field population (△); and *Z. luxurians* field populations (*), Honduras population (★), controlled

TABLE 5. Mahalanobis's distances among populations graphed on Figure 10. Data given below are the means (and ranges) for pairwise interpopulation distances, grouped by taxa.

Taxa	*Zea luxurians*	*Zea mays* ssp. *mexicana*	Race Nobogame	*Zea mays* ssp. *parviglumis*
Number of populations	4	2	1	5
Zea luxurians	3.1			
Zea mays ssp. *mexicana*[1]	7.2 (6.5–7.9)	4.1		
Race Nobogame	10.0 (9.7–10.4)	6.1 (5.4–6.9)	—	
Zea mays ssp. *parviglumis*	10.5 (8.9–12.0)	6.9 (5.5–8.1)	5.7 (5.3–6.3)	3.4

[1] Excluding race Nobogame.

On the lower portion of Figure 12, the *Zea perennis* population composed of plants cultivated from seeds and rhizomes collected by Collins in 1921 shows no closer relationship to Collins's field specimens from the same locality than to the perennial teosinte populations from other stations. In fact, this field collection of *Zea perennis* from Ciudad Guzman is separated by a greater distance from its corresponding cultivated population ($\bar{D} = 6.0$) than from the La Ventana population of *Z. diploperennis* ($\bar{D} = 5.2$). Here then, two samples from the same local population fail to cluster closest to one another due to differences in the environments in which they grew.

Figure 13, which includes the two wild subspecies of *Zea mays*, shows a pattern of variation similar to Figure 12, with the cultivated populations of each subspecies separating slightly from its field populations. On Figure 13 some field populations of *Z. mays* ssp. *mexicana* are closer to garden populations of *Z. mays* ssp. *parviglumis* than they are to garden populations of their own subspecies. Again, this suggests that, at the subspecific level of evolutionary differentiation in *Zea*, genetic differences can be easily obscured by environmental modifications of the phenotypes. The characters which seem to vary most between field and garden populations of both *Z. luxurians* and *Z. mays* are vein number and spikelet width, the ratio of vein number to spikelet width being larger for garden grown plants.

Finally, Figure 13 shows that the annual teosinte population from southwestern Jalisco recently discovered by Guzman (1978) at La Huertita near Casimiro Castillo clusters with *Z. mays* ssp. *parviglumis*. This suggests that this population belongs in *Z. mays* ssp. *parviglumis*, a conclusion supported by their similar vegetative morphologies and the fact that the La Huertita population, like other ssp. *parviglumis* populations, grows in seasonally moist habitats with rainfall in excess of 1,200 mm annually (Doebley, 1984).

SUMMARY OF RESULTS

The preceding analysis of tassel and spikelet morphology shows that the genus can be divided into sections *Luxuriantes* and *Zea*. The former section is characterized by few tassel branches, a short branching axis, short internodes on the tassel branches, and highly nerved outer glumes on which the prominent lateral nerves are developed into wings near the apex of the spikelet. Section *Zea*, on the other hand, is characterized by a larger number of tassel branches, a longer branching axis, longer internodes on the tassel

←

garden populations (□) and uncontrolled garden population (◇).—13. 9 field, 8 controlled garden and 3 uncontrolled garden populations of the wild taxa of *Zea mays* including *Z. mays* ssp. *mexicana*, 5 field populations (+) and 2 garden populations (X); *Z. mays* ssp. *mexicana* race Nobogame, field population (★) and 2 garden populations (Y); and *Z. mays* ssp. *parviglumis*, 4 field populations (△), 5 garden populations (□) and the LA HUERTITA, Jalisco population (◇).

branches, and fewer-nerved outer glumes that lack wings. Within sect. *Luxuriantes, Zea luxurians* is completely distinguished from the perennials on the basis of its much more numerously nerved outer glumes with smaller apical wings and slightly greater number of tassel branches. *Zea diploperennis* and *Z. perennis* could not be distinguished on the basis of tassel morphology. Within sect. *Zea,* the wild populations (teosintes) can be divided into two groups corresponding to *Z. mays* ssp. *mexicana* and ssp. *parviglumis.* On the canonical variate analysis graphs, these two subspecies showed a small area of overlap for field data but no overlap for plants grown in a uniform garden. For both the field and garden data, the two subspecies were distinguished in that *Z. mays* ssp. *mexicana* has fewer branches, a shorter branching axis, and larger spikelets and anthers than *Z. mays* ssp. *parviglumis.* Within *Z. mays* ssp. *mexicana,* races Central Plateau, Chalco, and Nobogame were completely indistinguishable for field data; however, for the garden data, race Nobogame separates from the other two. Garden specimens of race Nobogame tend to have fewer tassel branches and smaller spikelets than typical *Z. mays* ssp. *mexicana.* This seems to be an artifact of its adaptation to the long days of northern Mexico, which forces it to flower prematurely in Florida. Within *Z. mays* ssp. *parviglumis,* no consistent differences were found between vars. *parviglumis* and *huehuetenangensis.* Finally, *Z. mays* ssp. *mays* was shown to differ from its two conspecific wild subspecies only on the basis of characters that could have been altered during the domestication process. These characters include the length of internodes on the central spike, which are shorter in maize, and the length of the spikelets, which are longer in maize. Internode length would have decreased as man selected for a condensed ear with a large number of grains. Male spikelet size would have increased as man selected for larger female spikelets (kernels). In both cases, the parallel variation in the tassel and ear results because these structures are homologous (Anderson, 1944a).

Illustration of Taxa

Iltis and Doebley (1980) provided a taxonomic synopsis of *Zea,* while Doebley and Iltis (1980) illustrated the male spikelets of *Zea* to some extent, providing a dichotomous key to the group. The goal here is to describe and illustrate further the taxa, with special reference to male floral morphology. Those aspects of vegetative and female inflorescence morphology that are essential to the circumscription of the taxa are also described. However, the female inflorescence, and especially its immensely complex branching patterns in the teosintes are slighted here, and are in need of a separate detailed study. Similarly, hybrids of the various teosintes and maize, although common in the field, are not described below.

Zea Linnaeus, Species Plantarum 971. 1753; Genera Plantarum, ed. 5, 419. 1754.

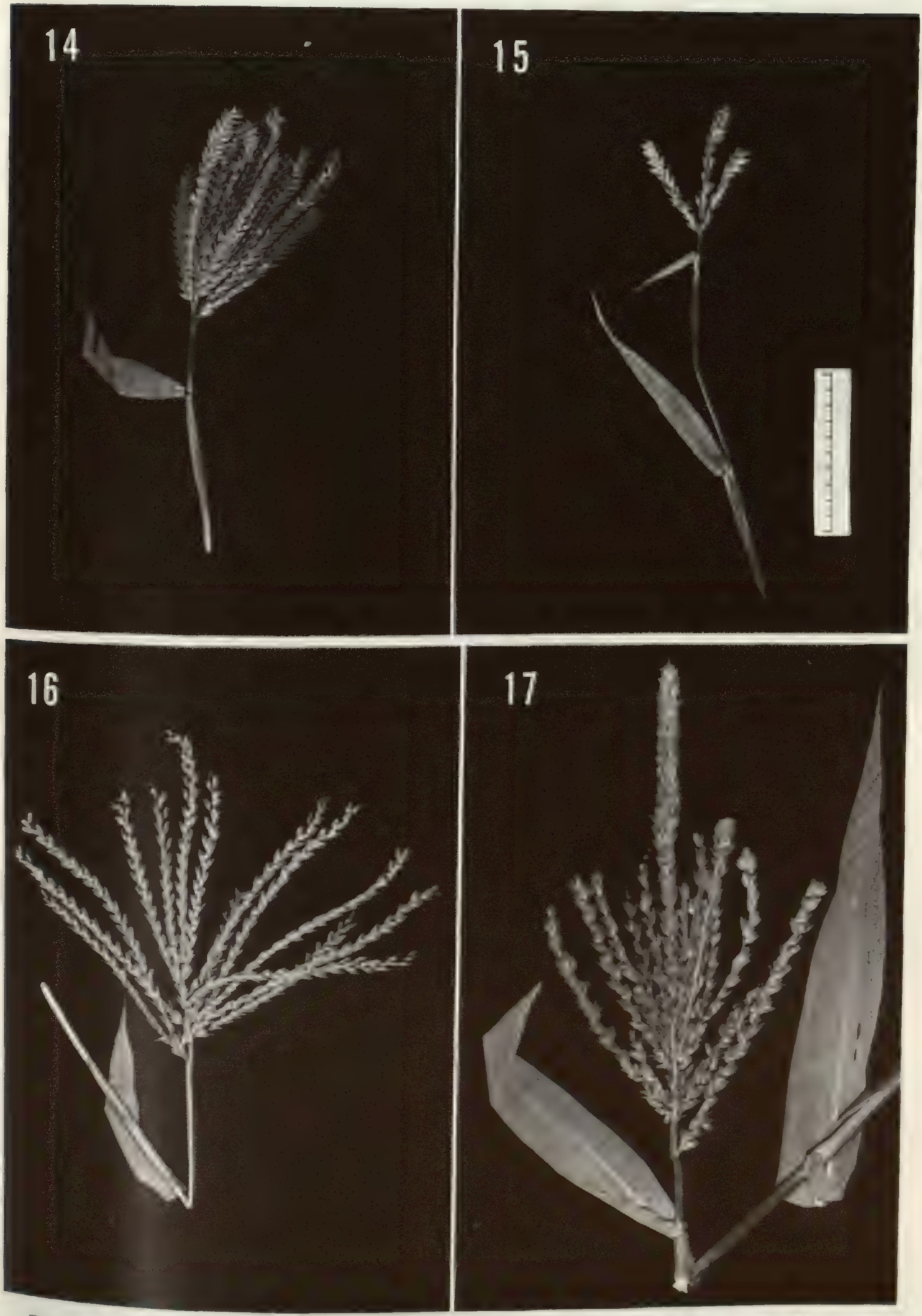
I. Section **Luxuriantes** Doebley and Iltis, Amer. J. Bot. 67: 982. 1980.

1. **Zea diploperennis** Iltis, Doebley, and Guzman, Science 203: 186. 1979.

Male inflorescences with (0–)3–13 ± divergent to nodding branches, these 6–15 cm long, 12–20 mm wide, the central spike barely exceeding the tassel branches in length (Fig. 14); *branching axis* 1–4 cm long; *spikelets* 8.5–11.5 mm long, in sessile-pedicellate pairs, these distichously arranged on the branches; *branch internodes* scaberulous with prominent abscission layers between them, broad (1 mm wide), in cross-section triangular with ciliate edges, and short (2–6 mm), the spikelets therefore crowded and overlapping (e.g. 14 spikelet pairs in 4 cm), with the tip of the sessile spikelet of each pair reaching the base of the next higher pair above on the same side (Figs. 22–23); *pedicels* scabrous, enlarged below the spikelet, 1.5–3.5 mm long; *glumes* of the spikelet glabrous (rarely scaberulous), sublustrous, often purple tinged, stiff and firm and somewhat brittle when old; outer glume flat on back and tightly enclosing the inner, strongly green-nerved, the nerves often clustered marginally near the apically ciliate prominent lateral wings (Fig. 37); inner glume keeled along the mid-nerve, scaberulous where it contacts the rachis.

Female inflorescences consisting of slender distichous spikes, each with 5–10 cupulate fruitcases, these trapezoidal-cylindric, 6–9 mm on the long side, 2.5–4.5 mm on the short side, 4–5 mm in diameter, when mature light sepia to grayish brown, and speckled with dark brown or nearly black; weight of 100 mature fruitcases 6.8–7.5 g.

Loosely clump-forming perennial, with both cord-like and tuber-like rhizomes, both of these with short (2–6 mm) internodes. Rare, endemic to Sierra de Manantlan, Jalisco, Mexico, alt. 1,400–2,400 m.



FIGURES 14–17. Pressed male inflorescences.—14. *Zea diploperennis, Iltis, Guzman, Doebley and Lasseigne 450* (plant GG).—15. *Zea perennis, Guzman s.n.* (plant I).—16. *Zea luxurians, K. Lind 421* (plant T).—17. *Zea mays* ssp. *mays* (Mexican Pyramidal), *Iltis and Doebley 405* (plant B). (Scale in cm.)

2. *Zea perennis* (Hitchcock) Reeves and Mangelsdorf, Amer. J. Bot. 29: 817. 1942.

Euchlaena perennis Hitchcock.

Male inflorescences similar to those of *Zea diploperennis,* except with fewer, (0–)3–8, erect or rarely somewhat nodding branches (Fig. 15), these 6–12 cm long, 10–20 mm wide; *branching axis* 1–2.5 cm long (see also Figs. 24, 25, 38).

Female inflorescences similar to those of *Zea diploperennis,* except with the fruitcases commonly gray or sepia, speckled with dark brown; weight of 100 mature fruitcases 8.3 g.

Densely sod-forming perennial, with cord-like rhizomes, these with long (1–6 cm) internodes. Rare, endemic to the vicinity of Cuidad Guzman, Jalisco, Mexico, alt. 1,520–2,200 m.

3. Zea luxurians (Durieu and Ascherson) Bird, Taxon 27: 363. 1978.

Euchlaena luxurians Durieu and Ascherson.

Male inflorescences with (0–)4–25 erect branches, these 7–20 cm long, 8–15 mm wide, the central spike often exceeding the branches in length (Fig. 16); *branching axis* 1–9 cm long; *spikelets* 8.5–12.5 mm long, in sessile-pedicellate pairs, these distichously arranged on the branches (Figs. 26–27); *branch internodes* densely scaberulous or strigose with prominent abscission layers between them, broad (1 mm wide), triangular in cross-section with ciliate edges, ± short (3–6 mm), spikelets therefore ± crowded and overlapping (e.g. 10 pairs in 4 cm) with the tip of the sessile spikelet of each pair reaching the base of the next higher pair above on the same side (Figs. 26–27); *pedicels* scaberulous or strigose, enlarged below spikelet, 1.5–3.8 mm long; *glumes* of the spikelet scaberulous, rough, stiff and somewhat brittle when old; outer glume flat on back, tightly enclosing inner glume, and having numerous (10–28) indistinct nerves between its two prominent ciliate lateral nerves, the latter produced into narrow wings apically (Fig. 39); inner glume with 5–12 nerves, keeled along midnerve.

Female inflorescences consisting of slender distichous spikes, each with 5–9 light brownish gray trapezoidal cupulate fruitcases, these 7–11.5 mm on long side, 3.7–6.5 mm on short side and 3–5 mm in diameter; weight of 100 mature fruitcases 7.6–9.9 g.

Robust annual, main culm usually highly branched and without any or only few tillers in the wild. Honduras, southeastern Guatemala (Provinces of Jutiapa, Chiquimula, and Jalapa), and southeastern Mexico (Oaxaca, San Augustin only), alt. 410–1,100 m.

II. Section **Zea**.

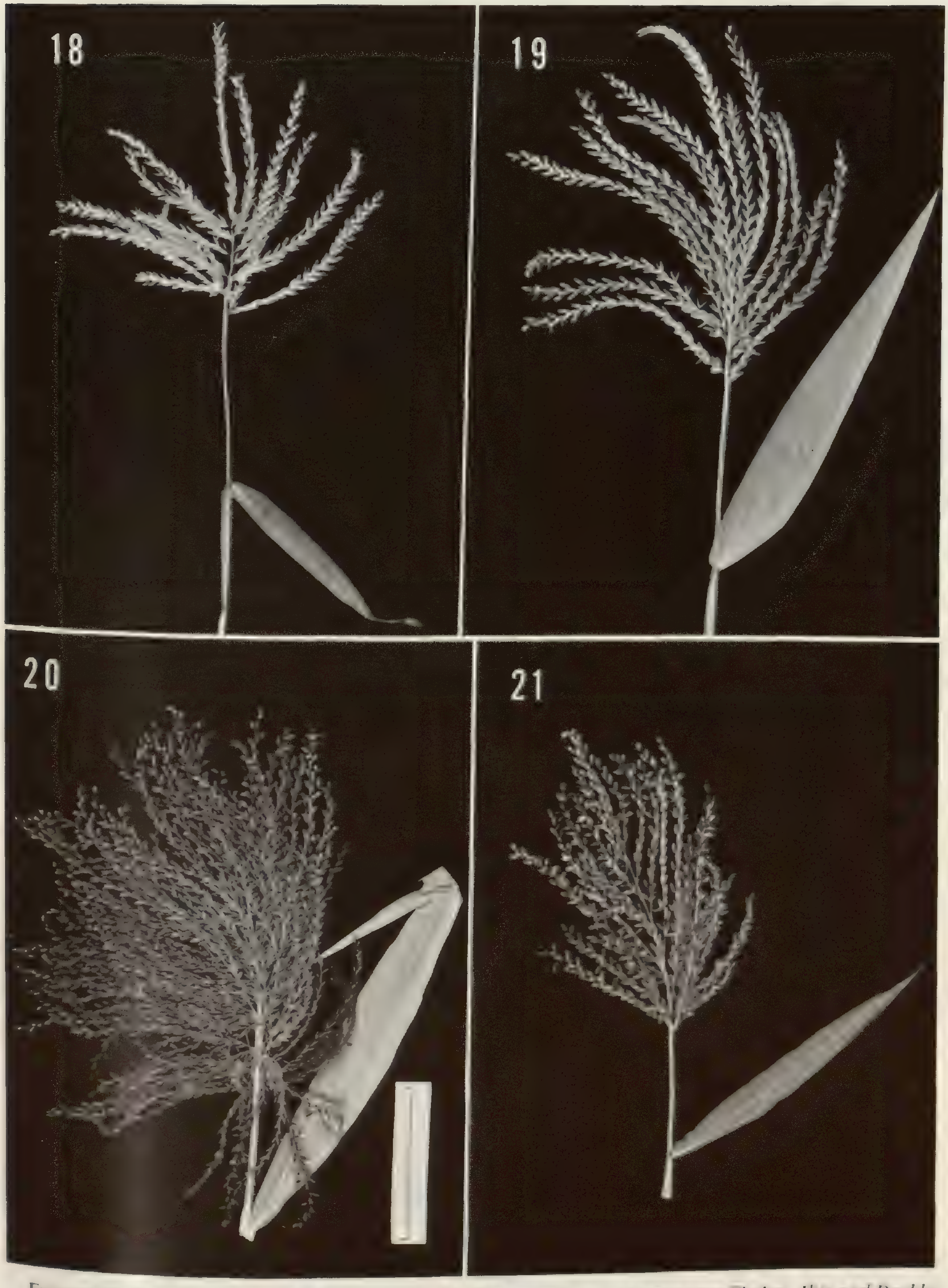
4. Zea mays Linnaeus, Species Plantarum 971. 1753.

Male inflorescences with numerous branches (in well grown plants many more than 12, except in certain races of cultivated *Z. mays*), these lax (stiff in some races of maize), the central spike occasionally somewhat stiffer, stronger, and more densely beset with spikelets than the tassel branches (this highly exaggerated in cultivated *Z. mays*) (Figs. 17–21); *branching axis* usually (1–)3–18 cm long; *spikelets* 4.6–13.0 mm long, usually in sessile-pedicellate pairs; *branch internodes* variously scabrous-pubescent, slender (less than 1 mm wide), rounded on the back, not strongly flattened, elongated (3.5–8.2 mm or more) (except in central spike of maize), spikelet arrangement therefore loose and open and with the tip of the sessile spikelet of each pair not reaching the base of the next higher pair above on the same side (Figs. 28–35); abscission layers between the internodes strongly to weakly developed (totally absent in *Z. mays* ssp. *mays*), the tassel branches therefore often tardily disintegrating (or not at all in maize); *pedicels* slender, 1–7 mm long; *glumes* of the male spikelet variously scabrous-pubescent, rounded on back, the outer glume only loosely embracing the inner one, both flexible and ± papery in texture; outer glume with few (6–15) veins, the two major lateral veins only slightly stronger than the secondaries between them and not winged; cilia along the keels hair-like and soft, and not scaberulous and tooth-like (Figs. 40–45); inner glume 3–8 nerved.

Female inflorescences either (in maize) a single massive polystichous spike (with occasional smaller subsidiary spikes), terminal on a lateral branch, or (in teosinte) consisting of slender distichous spikes, these composed of 5–12 or more ± triangular cupulate fruitcases.

4a. Zea mays L. ssp. **mays**.

Male inflorescences highly variable, with (0–) 3–30 or more branches, these 5–30 cm long, the central spike almost always strongly distinguished from the tassel branches (Fig. 17); *spikelets* 6–13 mm or more long, in sessile-pedicellate



FIGURES 18–21. Pressed male inflorescences.—18. *Zea mays* ssp. *mexicana* race Chalco, *Iltis and Doebley 9* (plant U).—19. *Zea mays* ssp. *mexicana* race Central Plateau, *Palmer 743*.—20. *Zea mays* ssp. *parviglumis* var. *parviglumis* (race Balsas), *Iltis and Doebley 362* (plant A).—21. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (race Huehuetenango), *Doebley 371* (cultivated in Homestead, Fla.). (Scale in cm.)

pairs, these distichously arranged on the lateral branches (Figs. 28–29) and polystichously arranged on the central spike (here single spikelets or groups of three spikelets are not uncommon, the pedicellate spikelet sometimes essentially sessile), the spikelets on the latter extremely crowded and overlapping (up to 26 or more spikelet pairs in 4 cm); *glumes* of the spikelet glabrous, scabrous, lanate, sericeous or villous (Fig. 40).

Female inflorescences consisting of a single terminal spike ("ear"), this polystichous (8–20 or more rows of grain), gigantic with 100–2,000 naked caryopses ("grains"), these, attached to a massive central axis ("cob"), laterally displaced from their reduced, collapsed, empty, and hidden cupules, the entire spike tightly enclosed in a series of 8–12 or more leaf sheaths ("husks"), all borne on a thick peduncle ("shank").

Monopodial or sparsely tillered annuals. World-wide cultigen.

4b. Zea mays L. ssp. **mexicana** (Schrader) Iltis in Annual Rev. Genet. 4: 450. 1971; Phytologia 23: 249. 1972; emended circumscription Amer. J. Bot. 67: 1001.

Male inflorescences with 0–20(–35) nodding branches, these 5–25 cm long, the central spike identical with to slightly larger than the tassel branches (Figs. 18–19); *spikelets* (6.6–)7.5–10.5 mm long, in sessile-pedicellate pairs, these distichously arranged on all branches (Figs. 30–31); *glumes* sparsely to densely scabrous (Figs. 41–43).

Female inflorescences consisting of slender distichous spikes; each spike consisting of 9–12 or more triangular cupulate fruitcases, the former enclosed in a single sheath and borne on a short to elongate slender peduncle; fruitcases 6–10 mm long, 4–6 mm wide, often pointed or "pinched" on the axial side, variable in color, gray, tan, or dark brown, and mottled or speckled with dark brown; weight of 100 mature fruitcases 5.6–10.4 g.

4b-I. Race Chalco of Wilkes.

Plants vegetatively robust, maize-like, generally with no or only few (1–6) tillers; leaf sheaths densely pilose and often dark red in color; leaves sparsely pilose; Valley of Mexico and its slopes, Mexico (cf. Wilkes, 1967), alt. 2,150–2,500 m.

4b-II. Race Central Plateau of Wilkes.

Essentially identical to race Chalco except leaf sheaths less densely pilose and not as deep red in color. Some populations are vegetatively somewhat depauperate and resemble race Nobogame. Michoacan, Guanajuato, and eastern Jalisco (cf. Wilkes, 1967), alt. 1,750–2,100 m.

4b-III. Race Nobogame of Wilkes.

Similar to race Chalco and especially race Central Plateau except the plants vegetatively less robust with fewer tassel branches, narrower and shorter leaves, and slightly smaller male and female spikelets, the male spikelets having a fewer-nerved outer glume. Nobogame, Chihuahua (cf. Wilkes, 1967), alt. ca. 1,900 m.

4c. Zea mays L. ssp. **parviglumis** Iltis and Doebley, Amer. J. Bot. 67: 1001. 1980.

Male inflorescences similar to those of ssp. *mexicana* except more delicately and often much more densely branched (up to 100 or more branches) with tertiary branching much more frequent (Figs. 20–21); *spikelets* markedly smaller than those of ssp. *mexicana* 4.6–7.2(–7.9) mm long (Figs. 32–35, 44–45), 1.6–2.8 mm wide.

Female inflorescences similar to those of ssp. *mexicana* except with fewer (5–10) triangular cupulate fruitcases per spike; fruitcases smaller (5.0–8.0 mm long, 3.0–5.0 mm wide) and blunt on the axial side; weight of 100 fruitcases 3.1–5.6 (–7.9) g.

4c-I. **Zea mays** L. ssp. **parviglumis** Iltis and Doebley var. **parviglumis**. Race Balsas of Wilkes.

Leaves commonly at least sparsely pilose to velvety pubescent, plants up to 3.5 m tall. Plants of thorn scrub and open summer-green tropical deciduous forest, as well as maize fields and their edges, on well-drained slopes of mountains and hills in the Rio Balsas valley of Guerrero, Michoacan, and Mexico at 600–1,600 m alt. (–1,950 m ? cf. Wilkes, 1967, p. 119), these in huge dense and clearly wild stands, and rarely in southwestern Jalisco at 400–1,200 m, this a distinct population with a moister ecology and later flowering date (Guzman, 1978, 1982); flowering from September through October, with ripe fruit by December.

4c-II. **Zea mays** L. ssp. **parviglumis** Iltis and Doebley var. **huehuetenangensis** Iltis and Doebley, Amer. J. Bot. 67: 1002. 1980. Race Huehuetenango of Wilkes.

Leaves essentially glabrous, plants up to 5 m tall, the tallest of all teosintes. Plants of old maize

FIGURES 22–23. Lateral branch segment of a male inflorescence of *Zea diploperennis, Iltis, Guzman, Doebley and Lasseigne 450* (plant GG).—22. Abaxial view.—23. Adaxial view. (Scale in mm.)

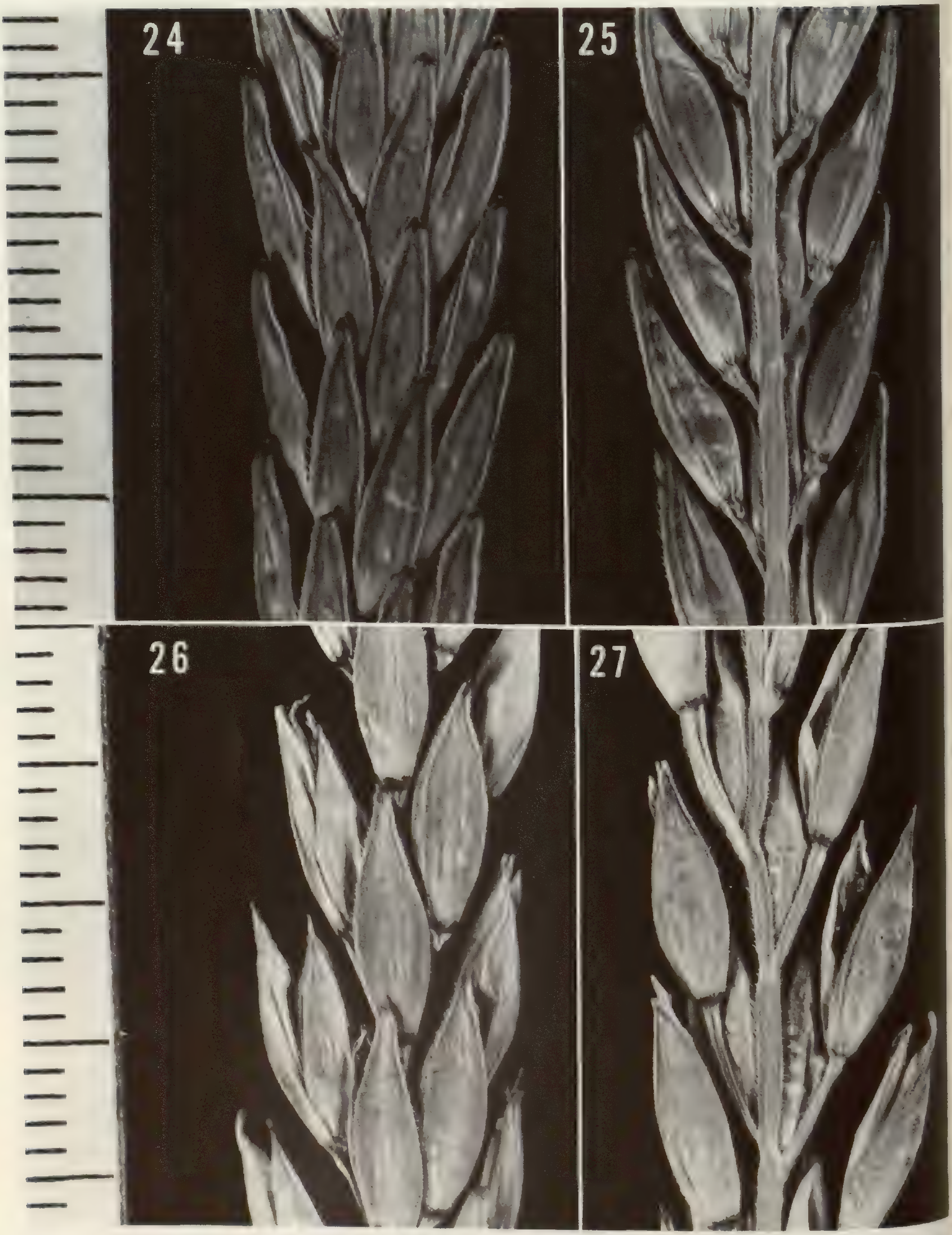
fields, edges of fields and oak forest, Province of Huehuetenanago, Guatemala, from 900–1,650 m alt. (fide Wilkes, 1967, p. 56); flowering from late November to January and fruiting from January through February, depending on the onset of the rainy season, which here, as in the habitat of the typical variety, is tremendously variable from year to year.

Since the time of its original description, it has been learned that *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* can be distinguished from the typical variety by its essentially glabrous leaves (see above). It has also been learned that, although the habitat of *Zea mays* ssp. *parviglumis* in the Balsas river valley is highly seasonal and extremely dry during the winter months, this region receives 120–160 cm of rainfall annually making it seasonally, at least, quite moist (Doebley, 1984). In this sense then, *Zea mays* ssp. *parviglumis* var. *parviglumis* (Balsas teosinte) occupies a habitat (seasonally mesic) similar to the mesic habitat of var. *huehuetenangensis*. This is not surprising, considering their similar morphologies.

The Phylogeny of *Zea*

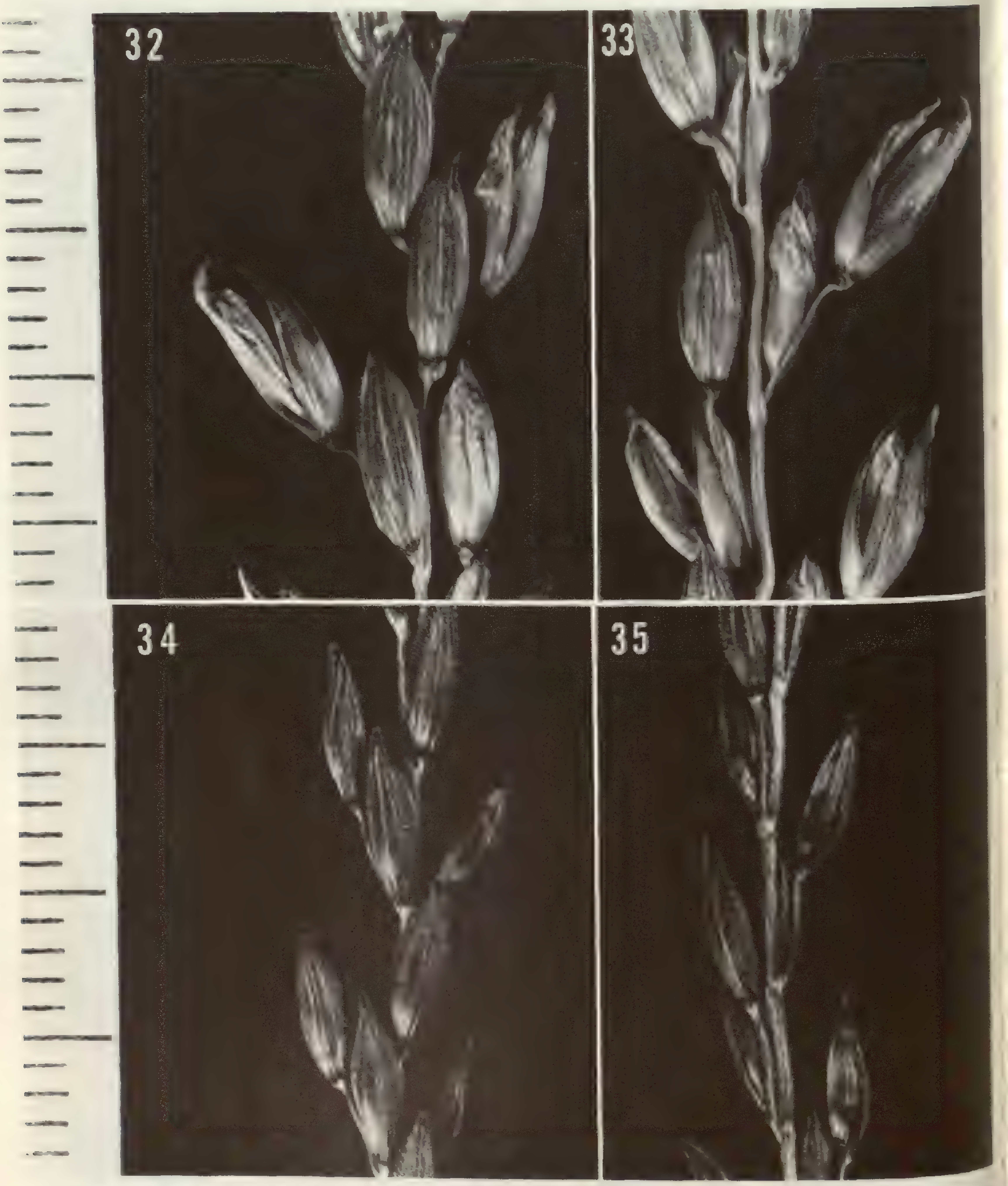
Little attention has been devoted to discussion the phylogeny of the teosintes, ostensibly because so few have regarded them as anything more than sporadic hybrids of maize and either *Tripsacum* or some hypothetical, primeval teosinte. The first of these ideas, the theory of Mangelsdorf and Reeves (1939), that teosinte is a maize-*Tripsacum* hybrid, has now been dismissed as untenable even by its author (Mangelsdorf, 1974). The various other proposals that racial diversity in teosinte represents nothing more than the incorporation of varying amounts of maize germplasm into some primitive teosinte still have their supporters. In this section I will examine the morphological and other evidence in relation to one of these theories, namely Wilkes (1979) and Mangelsdorf's (Wilkes & Mangelsdorf, 1979; Mangelsdorf et al., 1981) most recent hypothesis that all the races of annual teosinte are the products of the hybridization of *Zea diploperennis* and maize. Further, I will articulate my own view that all the teosinte taxa represent the products of adaptive radiation and geographic speciation with only minor if any maize introgression.

If one believes with Wilkes and Mangelsdorf that the annual teosintes were conceived through the miscegenation of maize and diploperennial teosinte, then they should exhibit intermediacy between these two taxa for at least some traits. Intermediacy may result from processes other than hybridization, and therefore cannot on its own establish the occurrence of hybridization. Nevertheless, intermediacy for at least some traits is a common outcome of hybridization. Thus,



FIGURES 24–27. Lateral branch segment of a male inflorescence.—24–25. *Zea perennis, Iltis, Puga, Guzman, Doebley and Lasseigne 550* (plant C).—24. Abaxial view.—25. Adaxial view.—26–27. *Zea luxurians, K. Lind 419*.—26. Abaxial view.—27. Adaxial view. (Scale in mm.)

FIGURES 28–31. Lateral branch segment of a male inflorescence.—28–29. *Zea mays* ssp. *mays* race Nal-Tel (cultivated in Homestead, Fla.).—28. Abaxial view.—29. Adaxial view.—30–31. *Zea mays* ssp. *mexicana* race Central Plateau, *Iltis and Doebley 96*.—30. Abaxial view.—31. Adaxial view. (Scale in mm.)



FIGURES 32–35. Lateral branch segment of a male inflorescence.—32–33. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* (race Huehuetenango), *Doebley 417* (cultivated in Homestead, Fla.).—32. Abaxial view.—33. Adaxial view.—34–35. *Zea mays* ssp. *parviglumis* var. *parviglumis* (race Balsas), *Iltis and Doebley 362* (plant A).—34. Abaxial view.—35. Adaxial view. (Scale in mm.)

one can check Wilkes and Mangelsdorf's hypothesis by inspecting the mean values for some important taxonomic traits of the taxa presumably involved in this event (Table 6). In order to give this hypothesis the best possible chance of validation, I have listed on this table two rather extreme forms of so-called "primitive" maize. Mangelsdorf, himself, has used one of these maize

races (Palomero Toluqueño) to test this hypothesis (Camara H. & Mangelsdorf, 1981).

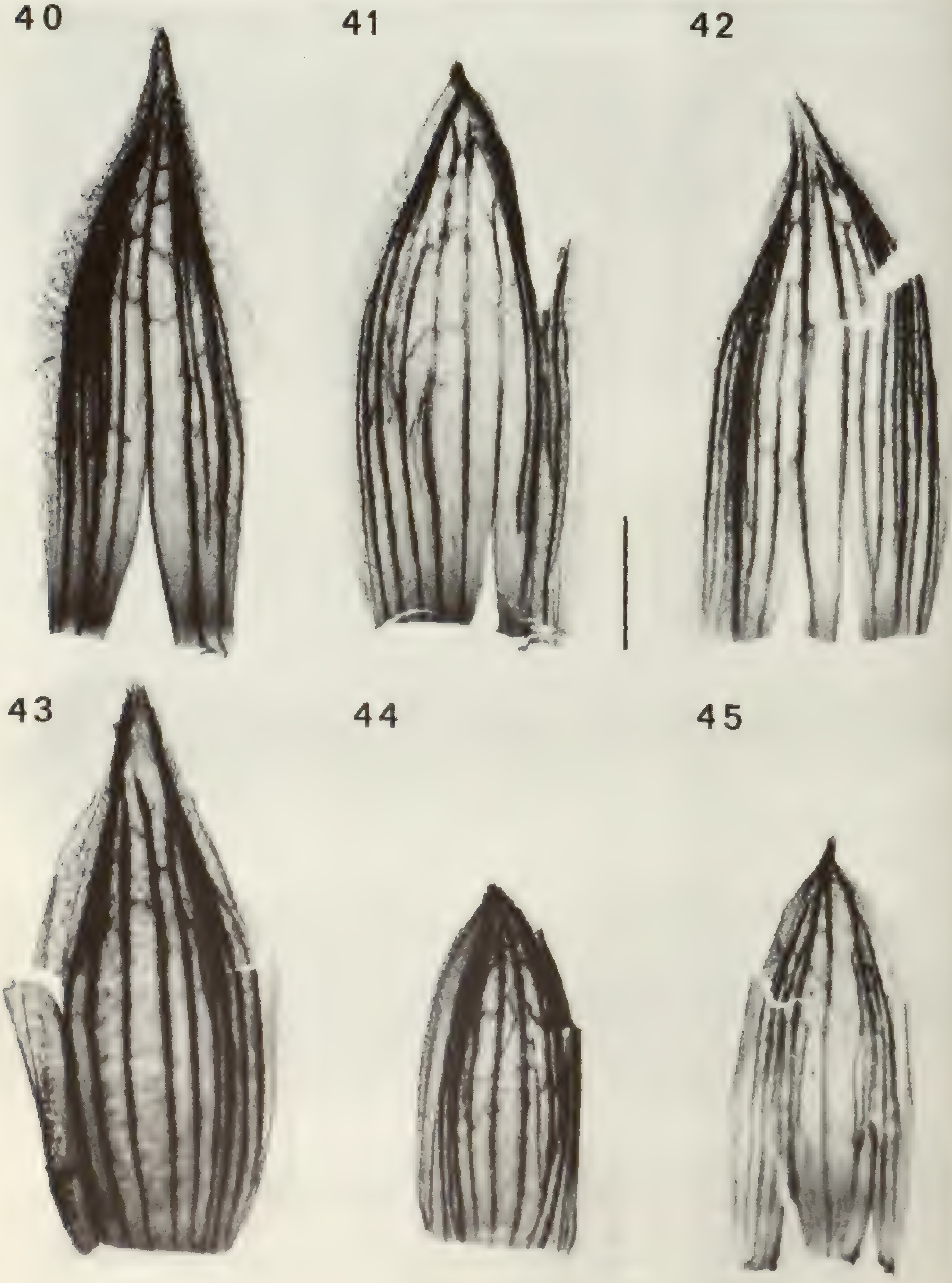
In Table 6, there is scarcely any evidence to bolster the theory of Wilkes and Mangelsdorf. For glume length, spikelet width, and vein number, all of the Mexican annual teosintes have small values outside of the range between *Zea diploperennis* and maize. For pedicel length and length of internodes on both the central spike and the lateral branches, all of the Mexican annuals have values larger than either maize or diploperennial teosinte. For caryopsis weight and central spike length, *Z. mays* ssp. *parviglumis* has values smaller than either of the two hypothetical "parental" species. For pedicel length, vein number, and length of internodes on the central branch, *Z. luxurians* has values outside of the range between diploperennial teosinte and maize. Clearly then these data in no way verify the hypothesis that the annual teosintes sprang forth from the hybridization of maize and *Z. diploperennis.*

On the other hand, if one cares to hypothesize that *Zea luxurians* and not *Z. diploperennis* fulfilled the role of the primeval pure teosinte involved in the hybridization with maize, the same difficulties arise. As can be seen from Table 6, the Mexican annual teosintes are no more intermediate between *Z. luxurians* and maize than they are between maize and *Z. diploperennis.* This conclusion is further supported by Figure 6 which demonstrates that the Mexican annual teosintes are in no way morphologically intermediate between maize and the teosintes of sect. *Luxuriantes.*

Other independent evidence also reflects disparagingly on Wilkes's hypothesis. First, analysis of isoenzymatic variation in *Zea* shows a large number of alleles restricted to sect. *Luxuriantes* and absent from all taxa of sect. *Zea,* as well as a close association between maize and Mexican annual teosinte, and thus, no evidence for the intermediacy of the annual teosintes (Doebley et al., 1984). Similarly, the seed proteins of the taxa of sect. *Zea* are electrophoretically identical to one another and different from those of *Z. luxurians* (Smith & Lester, 1980). Further, the electrophoresis of DNA from chloroplasts and mitochondria reveals substantial variation in banding patterns with most species and subspecies having their own distinctive pattern (Timothy et al., 1979; Timothy et al., 1982). The tremendous diversity of cytoplasm DNAs is especially damaging to Wilkes and Mangelsdorf's hypothesis, because these DNAs have strict maternal inheritance, so their diversity can be explained only by gradual evolution. Hybridization could not have been involved.

FIGURES 36–39. Outer glumes of *Tripsacum* and teosinte.—36. *Tripsacum australe* from Peru (cultivated at Fairchild Tropical Garden Redlands Nursery, Row 44 Space 2, FG67-257).—37. *Zea diploperennis, Iltis, Guzman, Doebley and Lasseigne 450* (plant O).—38. *Zea perennis, Iltis, Puga, Guzman, Doebley and Lasseigne 550* (plant V).—39. *Zea luxurians, Doebley 376* (cultivated in Homestead, Fla.). (Bar = 2 mm.)

Much more sense can be made of the available information on variability in *Zea* if we simply treat the various taxa of this genus as the products of allopatric, geographic speciation and adaptive radiation. First, morphological evi-



FIGURES 40–45. Outer glumes of *Zea mays* sensu lato. —40. *Zea mays* ssp. *mays* race Chapalote (cultivated in Homestead, Fla.). —41. *Zea mays* ssp. *mexicana* race Chalco, *Doebley 374* (cultivated in Homestead, Fla.). —42. *Zea mays* ssp. *mexicana* race Central Plateau, *Doebley 375* (cultivated in Homestead, Fla.). —43. *Zea mays* ssp. *mexicana* race Nobogame, *Doebley 370* (cultivated in Homestead, Fla.). —44. *Zea mays* ssp. *parviglumis* var. *parviglumis*, *Doebley 372* (cultivated in Homestead, Fla.). —45. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis*, *Doebley 371* (cultivated in Homestead, Fla.). (Bar = 2 mm.)

TABLE 6. A comparison of maize and teosinte for some important taxonomic traits (field specimens only). All measurements are in mm unless otherwise noted. For a key to character acronyms see Materials and Methods.

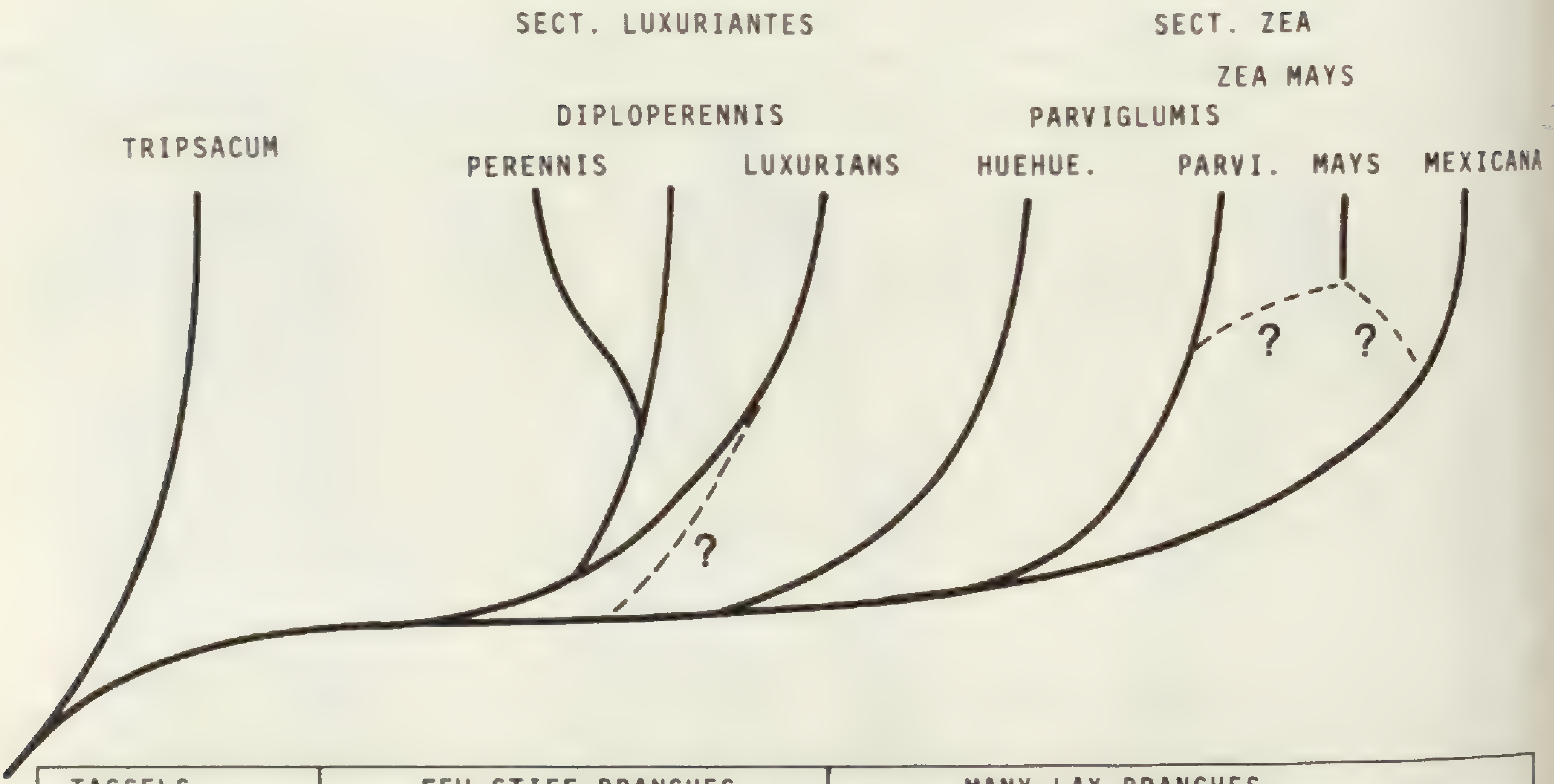
	Taxa					
					Zea mays	
Characters	*Zea diploperennis*	*Zea luxurians*	*Zea mays* ssp. *parviglumis*	*Zea mays* ssp. *mexicana*	Nal-tel	Palomero Toluqueño
9 GLUM-L	9.3	9.8	6.1	9.0	9.0	11.9
6 SPIK-W	2.7	2.5	1.8	2.5	2.6	3.5
7 PEDI-L	2.2	2.7	4.3	4.2	1.9	1.8
13 SHD-V#	7.2	12.7	2.5	3.4	3.2	3.3
14 TOT-V#	16.3	21.2	8.1	10.6	11.1	10.9
Caryopsis wt. (mg)	27.0	36.0	23.0	42.0	70.0	145.0
1 BRAN-#	6.5	13.3	22.1	19.7	42.2	2.8
4 CSIN-L	3.2	4.4	5.1	5.2	1.9	1.6
5 LBIN-L	3.1	4.5	5.8	6.0	5.2	4.8
2 CNSP-L	114.6	136.4	99.5	136.3	221.6	261.7
3 BRAX-L	23.8	45.3	73.5	86.5	166.5	15.2

dence presented in this paper demonstrates that *Zea* divides into two clearly defined groups, sections *Luxuriantes* and *Zea* (Fig. 46). Data from isozymes (Doebley et al., 1984), cytoplasm genomes (Timothy et al., 1979), seed proteins (Mastenbroek et al., 1981), and cytology (Pasupuleti & Galinat, 1982) support this division of the genus. Of these sections, sect. *Luxuriantes,* which rather closely resembles the related genus *Tripsacum,* is undoubtedly the more primitive. The many morphological features held in common by *Tripsacum* and sect. *Luxuriantes,* but lacking in sect. *Zea,* bespeak the phyletic affinities between these two taxa. These features include typically many-nerved, flattened outer glumes of the male spikelets with two prominent lateral nerves developed into wings (Figs. 36–39), short, thick internodes in the male portion of the inflorescence, trapezoidal fruitcases, perennial rhizomatous root system, and weakly monopodial habit. Further, *Tripsacum* and sect. *Luxuriantes* characteristically have many terminal heterochromatic regions on their chromosomes (Doebley & Iltis, 1980; Pasupuleti & Galinat, 1982).

After this initial and probably quite ancient divergence of sections *Luxuriantes* and *Zea,* diversification continued within each of these two taxa. Within sect. *Luxuriantes, Zea luxurians* probably separated quite early from the perennials. It might have abandoned the perennial habit as an adaptation to the dry and highly seasonal environment in southeastern Guatemala. The divergence between *Z. diploperennis* and *Z. perennis* apparently came somewhat later by means of autopolyploidy (Shaver, 1962; Galinat, 1971).

Within section *Zea, Z. mays* ssp. *parviglumis* var. *huehuetenangensis* is probably the most primitive taxon (Fig. 46). Evidence for this conclusion comes in part from cytology. Kato (1976; cf. Longley, 1941b) has shown that this teosinte has many terminal heterochromatic regions (knobs) like the teosintes of sect. *Luxuriantes.* Further, isoenzymatic data show this teosinte to have substantially diverged from the other taxa of section *Zea* (Doebley et al., 1984). On the other hand, tassel morphology (this paper), cytoplasm genomes studies (Timothy et al., 1979), and seed protein work (Smith & Lester, 1980; Mastenbroek et al., 1981), all show the clear relationship of this teosinte to the other teosintes of sect. *Zea* and to maize. Thus, it seems that *Z. mays* ssp. *parviglumis* var. *huehuetenangensis* is to some degree intermediate between the two sections though clearly belonging to section *Zea* (Fig. 46). Given the extent of the genetic distinctiveness of this variety, it might best be elevated to a subspecies.

Zea mays ssp. *parviglumis* var. *huehuetenangensis* shows its closest relationship to *Z. mays* ssp. *parviglumis* var. *parviglumis,* although these two teosintes are distinct both in terms of their genetics and their vegetative morphology. They are in part distinguished by the many internal heterochromatic regions (knobs) found on the chromosomes of the typical variety but lacking



TASSELS	FEW STIFF BRANCHES	MANY LAX BRANCHES	
SPIKELETS	FLAT ON BACK & WINGED	ROUNDED ON BACK-NO WINGS	
GLUMES	STIFF & BRITTLE	FLEXIBLE & ± PAPERY	
FRUITCASE	TRAPEZOIDAL	BLUNT TRIANGULAR	ACUTE TRIANGULAR
HABIT	MUCH TILLERED PERENNIALS	MONOPODIAL ANNUALS	
CHROMOSOMES	KNOBS TERMINAL	KNOBS TERMINAL & INTERNAL	

FIGURE 46. A phylogeny for *Zea* that is supported by much of the available data. Dashed lines indicate possible alternative pathways. While the figure seems to indicate *Z. mays* ssp. *mays* has acutely triangular fruitcase, the fruitcase is essentially absent from maize, being represented only by the cupules which are hidden within the ear.

on those of Huehuetenango teosinte (Fig. 46). They are similar in tassel morphology (this paper), seed proteins (Mastenbroek et al., 1981), and cytoplasm genomes (Timothy et al., 1979). These two varieties also share an adaption to a somewhat similar environment and this may partially account for their similar inflorescences. Both grow in low altitude (400–1,600 m), warm, seasonally moist sites with a long growing season. As discussed by Doebley (1984), the small seeds, glabrous, green or dilute red sheaths, small male spikelets, and many tassel branches characteristic of these two varieties may be adaptions to warm, moist environments. The typical variety is most common in the Balsas river valley; however, subpopulations of it inhabit similar environments in the lower, tropical deciduous forest of southwestern Jalisco, Mexico. *Zea mays* ssp. *parviglumis* var. *huehuetenangensis* is disjuncted from the Mexican population, occurring in the moist, warm montane oak forest of western Guatemala—the wettest of all teosinte stations.

The next group to diverge in Fig. 46 is *Z. mays* ssp. *mexicana*. This subspecies shows a much different adaptation than *Z. mays* ssp. *parviglumis*. It has colonized the higher, colder, drier sites with a shorter growing season, and is characterized by large seeds, red hairy sheaths, large male spikelets, and fewer tassel branches as an adaptation to this environment (Doebley, 1984). This subspecies includes three extant populations defined by Wilkes (1967): (1) race Chalco, the most extreme form adapted to the highest, coldest habitat of any teosinte, (2) race Central Plateau, adapted to the slightly lower, dry Meseta Central and (3) race Nobogame, a highly local population of the high, arid, short-seasoned Tarahumare Valley.

Despite the diametrical ecologies of the two subspecies, *Z. mays* ssp. *mexicana* and ssp. *parviglumis* var. *parviglumis* show some genetic similarities as compared to Huehuetenango teosinte. Both have internal chromosome knobs (Kato, 1976) and they are similar though distinct

isoenzymatically (Doebley et al., 1984). Figure 46 indicates this affinity in that ssp. *mexicana* and ssp. *parviglumis* var. *parviglumis* are placed near one another.

Although the evolutionary scheme just outlined best accommodates the morphological and other information, other possibilities cannot be entirely dismissed. For example, *Zea luxurians*, while being related to the perennials, may also be the ancestor of the other annual teosintes. As indicated by the dashed line on Figure 46, *Zea luxurians* may have emerged from the mainstock of *Zea* after the perennials and then the other annuals may have evolved from it. Although this scheme requires the annual habit to be derived only once, one would expect a closer relationship between *Z. luxurians* and *Z. mays* sensu lato were this system correct. In fact, its annual habit notwithstanding, *Z. luxurians* shows no closer relationship to *Z. mays* than does *Z. diploperennis*. Indeed, the many-nerved outer glumes, highly elongate trapezoidal fruitcases, and large terminal chromosome knobs of *Z. luxurians* show it to have diverged further from sect. *Zea* than the perennials.

Whence Came Maize?

The origin of maize has puzzled botanists, archaeologists, and others for over a hundred years. During this time many authors have supported either the view that maize evolved from a polystichous wild maize (Mangelsdorf, 1974; Randolph, 1976; Wilkes, 1979; Bird, 1980) or that teosinte is the ancestor of maize (Beadle, 1939, 1972, 1980; Langham, 1940; Longley, 1941a; Darlington, 1956; Miranda Colin, 1966; Iltis, 1971, 1972, 1983; Galinat, 1971, 1975; DeWet & Harlan, 1972; Harlan et al., 1973; Kato, 1976; Senadhira, 1976; Doebley & Iltis, 1980). Although in recent years the tide of opinion has moved in favor of the latter theory, the opponents of the teosinte theory have not regarded this trend with equanimity and the subject remains controversial. In the following discussion I will review the implications of the present study to this debate.

As mentioned above, any explanation of the origin of maize must of necessity provide an understanding of diversity among the teosintes. So, if the teosintes are nothing more than fortuitous hybrids of some ancient polystichous wild maize and *Tripsacum*, it would be quite reasonable to conclude that maize evolved from maize and not teosinte. Yet, the existence of such a wild maize has never been documented, and more importantly, the teosintes are quite clearly not hybrids of maize and *Tripsacum*. Similarly, if we hypothesize as Wilkes (1979, p. 12) has that prior to man's meddling there were only two forms within the genus *Zea*, (1) *Z. diploperennis*, the primitive *Tripsacum*-like perennial, and (2) *Z. mays*, the polystichous wild maize, and that these two forms hybridized to produce the annual teosintes, we will find ourselves equally besieged with difficulties. First, it seems unlikely that polystichy, a trait of obvious utility to man, arose in the wild among this group of grasses, the Andropogoneae, in which distichy is the universal rule, while the distichous wild relatives of maize, the annual teosintes, arose under domestication when maize crossed with *Zea diploperennis*. In this sense Wilkes's theory turns the most probable explanation inside-out by having the domesticated species emerge in the wild and the highly successful wild taxa emerge under domestication.

A much more parsimonious interpretation of the facts is to view the distichous taxa, the teosintes, as the products of natural selection within the purely distichous Andropogoneae, and the anomalous polystichy of maize that is found only in the cultigen as the utilitarian artifact of domestication (Doebley & Iltis, 1980). The present study supports this view by revealing teosinte (*Zea*) to be a genus with a relatively complex internal structure, as foreshadowed by Wilkes (1967), and one in which each population is genetically and morphologically sculptured to meet the demands of its particular environment.

In addition to implicating teosinte as the direct ancestor of maize, the biosystematic data aid in pinpointing the exact locality in which the cultivation of maize began. If one considers the morphological evidence, the teosintes of sect. *Luxuriantes* must be immediately dismissed as potential progenitors of maize, because their characteristic many-nerved, winged outer glumes and flattened male spikelets are unknown in this cultigen. The genetic evidence discussed in the previous section also enables us to rule out *Z. mays* ssp. *parviglumis* var. *huehuetenangensis* as a possible ancestor of maize. Of the remaining taxa, *Z. mays* ssp. *mexicana* and ssp. *parviglumis* var. *parviglumis*, the former shows the closest morphological relationship to maize (see Results). Certain populations of race Central Plateau in particular display the smallest Mahalanobis's distances from race Nal-Tel of *Z. mays* ssp. *mays*.

Although this suggests that maize could be domesticated *Z. mays* ssp. *mexicana* race Central Plateau, the nature of the resemblance cautions us to look more closely. *Zea mays* ssp. *mexicana* displays greater affinity to maize than does *Z. mays* ssp. *parviglumis* primarily because of its larger spikelets and fewer tassel branches. As these two traits have themselves undergone considerable transformation during the domestication process, they can provide only flaccid evidence on which to pinpoint either *Z. mays* ssp. *mexicana* or ssp. *parviglumis* as the ancestor of maize.

Other available data augment the morphological evidence. First, the isoenzymatic work of Senadhira (1976, Fig. 12) showed that some populations of Balsas teosinte (*Zea mays* ssp. *parviglumis*) cluster closest to the maize races Chapalote and Arrocillo Amarillo. Another isoenzymatic study involving a broader sample of teosintes also suggested maize to be closest to Balsas teosinte (Doebley et al., 1984). Kato's (1976) cytological studies revealed that both B chromosomes and abnormal chromosome 10 (type I), which are relatively common in Mexican maize races, co-occur only in teosinte from the Balsas region and are unknown in the Chalco area. This again points to the Balsas river drainage as the cradle of maize domestication.

Thus, most genetic data are consistent with the theory that maize arose from Balsas teosinte, while morphology would suggest that *Z. mays* ssp. *mexicana* is closest to maize. Prudence would advise that further information be gathered before rendering a final verdict.

While it has long been recognized that the biosystematic evidence points to teosinte as the ancestor of maize, the archaelogical evidence available apparently does not. The earliest archaeological maize specimens recovered from Tehuacan possess long soft glumes, a narrow flexible rachis, and shallow non-indurate cupules (Mangelsdorf, 1974), traits which would be difficult to derive from the female teosinte spike. It is for this reason, among others, that Mangelsdorf and his supporters have remained adamant in their belief that maize evolved not from teosinte, but from a "wild maize." Recently, Iltis (1981, 1983) has proposed a new theory, his Catastrophic Sexual Transmutation Theory, which attempts to explain both the biosystematic and archaeological evidence. Quite simply, he suggests that the teosinte female spike is *not* the ancestor of the maize ear, as has long been thought, but rather that the *central spike of the teosinte tassel,* which normally terminates a lateral branch, gave rise to the familiar maize ear. This new theory draws in part from older theories on the origin of the maize ear (Kellerman, 1895; Montgomery, 1906; Iltis, 1911; Weatherwax, 1918).

This theory has an initial appeal to the morphologist because the maize ear is terminal on a lateral branch, a position which in teosinte is usually occupied by a tassel. Thus, the early domestication of maize would have involved a sex change of the central spike of the terminal tassel on the lateral branches from male to female. Iltis believes this change and the subsequent (or concurrent) condensation of the central spike into the maize ear happened rapidly; thus we have the *Catastrophic Sexual Transmutation Theory.*

The aspect of this theory that most stirred my imagination was its implications for the archaeological specimens from Tehuacan. As described above, they do not fall neatly into a sequence between the teosinte female spike and the maize ear. However, under Iltis's theory, they are exactly the intermediates one would predict. The central spike of the teosinte tassel has a flexible rachis, shallow non-indurate cupules, and spikelets with long soft glumes [much like Mangelsdorf's (1974) ancestral pod-corn!], all characters of the Tehuacan specimens. Further, the central tassel spike of teosinte has two functional spikelets per node (cupule) as does the maize ear but unlike the teosinte ear, so that by applying Iltis's theory the reactivation of a suppressed spikelet is not necessary (cf. Beadle, 1972).

While the *Catastrophic Sexual Transmutation Theory* has some attractive features, it needs experimental verification. The developmental morphology of the male and female inflorescences of *Zea* should be studied with this theory in mind. Such work might not only resolve the origin of the maize ear, but may also provide a yardstick for the assessment of primitive versus advanced traits of the ear. Such a yardstick has been sadly lacking in all studies of racial variation in maize to date.

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APPENDIX A. Means (and standard deviations) for all characters and all populations. For key to population and character numbers see Materials and Methods. All measurements are in millimeters except characters 15, 16 and 17 which are in microns.

Character	Population							
	1	2	3	4	5	6	7	8
1	6.5 (2.7)	3.8 (1.2)	4.5 (1.1)	11.8 (6.1)	13.6 (7.2)	14.5 (5.2)	10.6 (6.7)	15.9 (8.1)
2	114.6 (15.5)	98.8 (8.1)	84.7 (9.4)	113.3 (25.0)	138.5 (29.5)	137.5 (19.2)	120.0 (42.0)	112.3 (29.0)
3	23.8 (11.7)	12.2 (5.6)	13.6 (5.7)	45.6 (25.1)	43.6 (13.4)	46.8 (16.3)	47.5 (25.0)	71.8 (26.6)
4	3.2 (.55)	3.1 (.43)	3.8 (.51)	4.7 (.67)	4.0 (.80)	4.5 (.49)	5.5 (1.22)	4.8 (1.83)
5	3.1 (.44)	2.9 (.32)	3.9 (.61)	4.6 (.83)	4.3 (.77)	4.5 (.60)	5.8 (.92)	5.9 (1.22)
6	2.7 (.18)	2.5 (.17)	2.4 (.23)	2.6 (.17)	2.5 (.09)	2.4 (.27)	2.5 (.31)	2.4 (.27)
7	2.2 (.57)	2.4 (.56)	2.7 (.60)	2.9 (.65)	2.6 (.45)	2.7 (.51)	4.1 (1.27)	4.1 (.63)
8	5.2 (.28)	4.9 (.21)	4.8 (.28)	5.2 (.42)	5.2 (.60)	4.8 (.29)	5.0 (.65)	4.8 (.49)
9	9.3 (.90)	9.9 (.48)	9.1 (.68)	10.2 (1.00)	9.5 (1.14)	9.7 (.69)	8.7 (.83)	8.6 (.75)
10	3.6 (.31)	3.4 (.16)	3.3 (.29)	3.7 (.23)	3.4 (.22)	3.4 (.22)	3.9 (.30)	3.2 (.27)
11	.312 (.038)	.390 (.056)	.299 (.046)	.188 (.039)	.200 (.052)	.196 (.028)	.024 (.028)	.024 (.034)
12	2.3 (.34)	1.6 (.26)	2.0 (.31)	2.3 (.22)	2.0 (.28)	2.0 (.30)	1.9 (.22)	1.9 (.32)
13	7.2 (1.01)	5.8 (1.15)	5.6 (1.42)	12.7 (1.56)	11.9 (2.30)	13.5 (1.43)	2.7 (.84)	3.2 (.92)
14	16.3 (1.33)	15.0 (1.07)	13.5 (1.42)	19.9 (1.59)	21.9 (1.89)	21.8 (1.94)	9.5 (1.58)	9.8 (1.13)
15	128. (14.6)	128. (16.6)	109. (12.2)	114. (15.3)	101. (9.2)	91. (16.2)	109. (13.3)	108. (15.2)
16	55. (11.6)	46. (8.4)	66. (12.9)	61. (8.2)	71. (6.9)	62. (12.7)	85. (18.0)	92. (27.7)
17	57. (15.9)	50. (12.3)	72. (11.1)	63. (7.9)	69. (4.9)	63. (12.3)	100. (17.6)	96. (14.0)

Character	Population							
	9	10	11	12	13	14	15	16
1	28.4 (12.7)	24.0 (6.7)	35.0 (21.5)	10.2 (5.5)	3.3 (1.5)	7.4 (3.7)	22.0 —	10.7 (7.7)
2	141.1 (27.8)	172.5 (28.2)	118.4 (29.2)	100.1 (23.1)	105.7 (20.0)	109.5 (26.5)	97.0 —	119.1 (48.6)
3	106.4 (42.8)	120.0 (21.6)	105.5 (36.4)	45.5 (26.7)	9.3 (8.0)	33.5 (23.0)	49.0 —	48.9 (37.0)
4	4.8 (.99)	5.6 (1.26)	5.3 (1.18)	5.2 (1.22)	4.3 (.44)	4.8 (.76)	4.9 —	4.4 (.63)
5	5.4 (.87)	6.8 (.97)	6.0 (.74)	6.5 (.81)	4.3 (.12)	4.4 (1.05)	4.6 —	4.8 (.71)

APPENDIX A. (Continued).

Character	Population 9	10	11	12	13	14	15	16
6	2.4	2.5	1.8	1.8	2.5	2.6	2.4	2.3
	(.34)	(.21)	(.21)	(.12)	(.07)	(.25)	—	(.22)
7	4.5	4.2	4.4	4.4	3.0	2.9	2.8	2.9
	(.99)	(1.08)	(.87)	(.77)	(.88)	(.74)	—	(.86)
8	5.3	5.5	3.7	3.9	5.1	4.7	4.8	4.7
	(.72)	(.60)	(.44)	(.29)	(.55)	(.45)	—	(.98)
9	9.1	9.6	6.0	5.8	9.5	9.5	9.8	8.1
	(.75)	(1.29)	(.55)	(.53)	(.29)	(.62)	—	(1.00)
10	3.7	3.3	2.9	2.6	3.4	3.6	3.4	3.4
	(.34)	(.33)	(.34)	(.34)	(.32)	(.27)	—	(.27)
11	.024	.040	.020	.026	.413	.156	.12	.049
	(.028)	(.033)	(.020)	(.027)	(.101)	(.033)	—	(.017)
12	1.7	1.8	1.5	1.3	2.1	2.0	1.7	1.7
	(.21)	(.26)	(.21)	(.12)	(.25)	(.28)	—	(.27)
13	2.9	4.8	2.1	2.2	6.7	11.3	14.0	2.9
	(1.02)	(1.32)	(1.00)	(1.01)	(2.08)	(2.83)	—	(1.27)
14	9.0	13.9	8.3	7.8	14.7	19.1	22.0	10.6
	(1.64)	(2.08)	(1.89)	(1.77)	(1.53)	(2.88)	—	(1.13)
15	112.	83.	87.	90.	121.	127.	110.	88.
	(14.9)	(9.2)	(16.6)	(8.7)	(9.3)	(15.0)	—	(12.4)
16	91.	73.	81.1	80.	68.	61.	40.	72.
	(20.6)	(9.6)	(18.2)	(10.6)	(10.7)	(7.6)	—	(10.2)
17	112.	79.	78.	91.	59.	66.	40.	84.
	(17.1)	(4.9)	(13.9)	(11.1)	(19.3)	(14.0)	—	(15.4)

Character	Population 17	18	19	20	21	22	23	24
1	5.7	16.6	16.6	12.0	16.0	15.5	13.5	8.3
	(1.5)	(7.5)	(5.3)	(4.3)	(3.6)	(6.4)	(9.0)	(2.5)
2	92.0	79.8	105.6	88.0	106.4	94.3	139.3	173.9
	(22.5)	(22.0)	(20.2)	(15.7)	(13.6)	(13.8)	(75.8)	(41.5)
3	36.0	69.4	62.6	56.0	59.5	66.5	61.7	57.5
	(7.0)	(31.3)	(14.3)	(15.2)	(10.8)	(23.4)	(27.4)	(22.6)
4	5.7	4.9	5.6	5.3	4.9	5.6	5.7	7.9
	(.93)	(.82)	(.82)	(.45)	(.82)	(.39)	(1.48)	(1.51)
5	5.3	4.8	6.2	5.7	5.5	6.4	6.7	7.8
	(.42)	(1.00)	(.85)	(.99)	(.30)	(.71)	(1.08)	(1.56)
6	2.4	1.9	2.9	3.1	2.9	2.8	3.0	3.1
	(.22)	(.29)	(.30)	(.16)	(.18)	(.24)	(.32)	(.39)
7	3.2	4.1	3.9	4.3	2.9	4.4	4.1	4.9
	(1.09)	(.96)	(.76)	(.82)	(.85)	(.78)	(2.34)	(.84)
8	4.7	3.9	5.1	5.1	5.2	5.3	5.9	5.8
	(.59)	(.57)	(.45)	(.49)	(.17)	(.29)	(.89)	(.71)
9	7.5	6.5	10.0	10.9	10.2	10.7	10.6	11.1
	(.57)	(.83)	(.50)	(.54)	(.58)	(1.08)	(1.43)	(1.69)
10	3.0	2.8	4.3	4.1	4.1	3.4	3.9	4.1
	(.26)	(.33)	(.38)	(.51)	(.29)	(.28)	(.72)	(.48)
11	.013	.020	.175	.185	.160	.160	.024	.064
	(.023)	(.020)	(.020)	(.056)	(.043)	(.042)	(.027)	(.042)

APPENDIX A. (Continued).

Character	Population 17	18	19	20	21	22	23	24
12	1.5 (.23)	1.4 (.25)	2.7 (.32)	2.4 (.53)	2.8 (.34)	2.2 (.20)	2.2 (.52)	2.4 (.40)
13	2.3 (1.15)	3.3 (.98)	15.6 (2.07)	14.3 (3.56)	15.8 (2.31)	14.2 (1.40)	3.7 (1.25)	5.9 (.80)
14	8.7 (1.15)	8.3 (1.42)	25.1 (2.53)	24.9 (3.56)	26.5 (1.69)	24.4 (2.07)	11.0 (3.09)	14.3 (1.45)
15	102. (9.3)	101. (19.0)	114. (11.9)	102. (9.9)	113. (9.2)	117. (13.3)	98. (9.0)	103. (15.5)
16	96. (19.4)	74. (12.5)	72. (9.6)	79. (11.0)	80. (8.5)	74. (8.8)	85. (13.5)	93. (15.7)
17	87. (10.7)	98. (22.9)	72. (13.8)	78. (8.5)	8.3 (11.6)	7.7 (7.7)	8.6 (15.7)	9.8 (14.8)

Character	Population 25	26	27	28	29	30	31	32
1	9.8 (4.0)	31.3 (12.2)	28.9 (9.9)	16.3 (7.5)	23.8 (7.2)	37.4 (12.1)	5.3 (3.9)	11.4 (5.5)
2	83.8 (19.0)	81.2 (18.5)	83.6 (19.1)	118.9 (44.6)	80.2 (18.8)	85.9 (40.6)	97.4 (17.4)	116.6 (37.5)
3	39.3 (11.7)	92.9 (22.8)	90.4 (22.7)	64.4 (25.2)	94.6 (15.4)	132.3 (16.4)	24.0 (24.6)	36.6 (15.1)
4	4.6 (.80)	5.4 (.49)	5.9 (.77)	6.6 (1.29)	5.7 (.43)	4.9 (.87)	3.5 (.68)	3.8 (.41)
5	5.2 (.63)	6.2 (.92)	6.8 (1.19)	7.0 (1.36)	6.0 (.67)	5.7 (1.05)	3.7 (.43)	4.0 (.55)
6	2.2 (.20)	2.1 (.25)	2.3 (.22)	2.0 (.13)	2.3 (.22)	2.2 (.33)	2.1 (.34)	2.2 (.12)
7	2.3 (.61)	4.4 (.82)	4.6 (.92)	5.3 (1.17)	5.4 (1.14)	4.0 (1.11)	2.2 (.60)	2.4 (.31)
8	4.1 (.65)	4.0 (.37)	4.0 (.43)	4.3 (.49)	4.7 (.42)	4.0 (.66)	4.0 (.60)	5.0 (.40)
9	7.4 (.59)	6.9 (.60)	7.2 (.34)	5.9 (.92)	7.7 (.74)	6.8 (.94)	8.4 (.48)	8.2 (.68)
10	2.7 (.42)	2.7 (.33)	2.9 (.28)	3.0 (.53)	3.2 (.29)	2.6 (.22)	2.8 (.30)	2.7 (.26)
11	.025 (.030)	.016 (.020)	.024 (.024)	.020 (.021)	.022 (.021)	.030 (.028)	.340 (.021)	.154 (.015)
12	1.4 (.30)	1.3 (.24)	1.5 (.18)	1.5 (.32)	1.5 (.15)	1.5 (.19)	1.4 (.27)	1.7 (.20)
13	2.6 (.74)	3.1 (1.09)	3.4 (1.28)	3.6 (1.41)	4.0 (1.26)	3.0 (.93)	8.6 (1.67)	12.3 (1.98)
14	8.1 (.83)	10.5 (1.88)	11.3 (2.34)	11.1 (1.64)	12.7 (1.70)	9.0 (2.20)	15.4 (1.23)	18.9 (2.67)
15	82. (6.9)	86. (12.4)	85. (9.0)	93. (11.1)	87. (10.1)	95. (12.9)	133. (25.0)	99. (27.8)
16	73. (10.5)	79. (11.0)	74. (7.1)	84. (13.1)	80. (9.5)	77. (12.9)	58. (18.0)	41. (10.5)
17	8.4 (15.3)	86. (10.2)	82. (11.3)	93. (7.0)	85. (11.7)	89. (18.6)	56. (15.4)	44. (8.8)

APPENDIX A. (Continued).

Character	Population 33	34	35	36	37	38	39	40
1	10.3 (4.3)	11.0 (9.8)	35.2 (11.1)	15.5 (3.5)	2.8 (.86)	42.2 (11.9)	7.4 (4.0)	4.9 (3.0)
2	121.7 (26.8)	97.4 (8.3)	67.7 (17.7)	85.5 (10.6)	261.7 (23.1)	221.6 (37.9)	311.1 (50.8)	258.4 (29.4)
3	48.3 (24.9)	37.6 (23.9)	98.8 (13.9)	91.5 (23.3)	15.2 (13.6)	166.5 (19.5)	52.6 (26.0)	26.4 (19.7)
4	5.6 (.81)	4.2 (.71)	4.7 (.47)	5.0 (.61)	1.6 (.35)	1.9 (.51)	2.6 (.82)	2.1 (.25)
5	5.1 (.56)	4.6 (.86)	6.3 (.61)	5.2 (.28)	4.8 (.82)	5.2 (.68)	5.0 (.49)	5.3 (.77)
6	2.6 (.42)	2.5 (.33)	2.1 (.15)	1.9 (0.0)	3.5 (.27)	2.6 (.23)	3.2 (.36)	3.0 (.17)
7	3.5 (1.09)	2.1 (1.21)	3.3 (.31)	6.0 (.18)	1.8 (.87)	1.9 (1.04)	2.8 (1.3)	2.9 (1.7)
8	5.3 (.62)	4.9 (.77)	4.1 (.51)	3.4 (.18)	6.8 (.48)	5.5 (.51)	7.1 (.49)	7.6 (.48)
9	10.9 (.97)	8.4 (1.16)	7.5 (.39)	6.8 (.35)	11.9 (.72)	9.0 (.71)	12.9 (1.30)	12.8 (1.19)
10	3.0 (.53)	3.3 (.37)	2.8 (.19)	2.7 (.09)	3.9 (.40)	3.8 (.31)	4.5 (.59)	4.0 (.61)
11	.173 (.033)	.008 (.017)	.033 (.030)	.020 (.028)	.028 (.024)	1.07 (.020)	.023 (.020)	.023 (.021)
12	1.8 (.27)	1.6 (.32)	1.5 (.15)	1.4 (.20)	2.0 (.32)	1.6 (.31)	1.8 (.32)	2.1 (.35)
13	13.0 (2.83)	2.8 (1.30)	3.8 (1.60)	3.5 (.70)	3.3 (1.13)	3.2 (1.11)	4.1 (1.55)	3.7 (1.60)
14	22.5 (3.56)	9.0 (2.12)	11.3 (1.75)	8.5 (2.12)	10.9 (1.88)	11.1 (2.06)	13.5 (2.25)	10.6 (1.62)
15	102. (11.7)	106. (24.3)	88. (7.8)	74. (13.1)	92. (8.6)	97. (11.3)	103. (16.0)	81. (12.8)
16	42. (15.2)	93. (16.1)	84. (19.5)	70. (6.6)	84. (10.2)	81. (12.0)	91. (9.6)	73. (11.3)
17	50. (12.7)	106. (22.4)	85. (18.1)	65. (0.0)	90. (12.7)	95. (13.6)	94. (14.0)	82. (13.6)

AN EMBRYOLOGICAL ANALYSIS OF MYRTALES: ITS DEFINITION AND CHARACTERISTICS[1]

Hiroshi Tobe[2] and Peter H. Raven[3]

Abstract

A combination of embryological characteristics clearly defines Myrtales as comprising Combretaceae, Lythraceae (including Punicaceae and Sonneratiaceae), Melastomataceae, Myrtaceae, Onagraceae, Oliniaceae, Penaeaceae, and Trapaceae, a circumscription that agrees with that of the "core" Myrtales given by Dahlgren and Thorne (1983). The ordinal characteristics are: 1) anther tapetum glandular, 2) ovule crassinucellate, 3) inner integument 2-layered (except in *Syzygium*), 4) micropyle formed by both integuments (except in *Syzygium* and *Trapa*), 5) antipodal cells ephemeral or absent, 6) endosperm formation Nuclear type and 7) seed exalbuminous. Haloragaceae, Lecythidaceae, and Thymelaeaceae definitely should be excluded from Myrtales on the basis of differences in three or more of these primary defining characteristics. On the other hand, embryological evidence does not contradict the possibility of a relatively close relationship between Elatinaceae and Myrtales, even though an overall consideration of their features seems to make such a relationship seem less likely. Embryological evidence indicates a considerable degree of heterogeneity in Rhizophoraceae, a family or group of families that is clearly not assignable to Myrtales.

Introduction

Although embryology has been an important source of evidence for the relationships of angiosperms for more than a century, both the tedious nature of the processes needed to prepare materials for embryological study and the difficulty of obtaining samples of key genera have retarded progress in this area. During the course of the past 50 years several authors including Schnarf (1931), Maheshwari (1950), and Davis (1966) have compiled the accumulated data on the embryology of angiosperms, and their books have been of use as guides to the literature. A number of other authors, including Maheshwari (1964), Davis (1966), Brewbaker (1967), and Philipson (1974), have evaluated the significance of individual characters or assemblages of characters in considering the relationships of different groups of angiosperms. In 1967, a symposium on the comparative embryology of angiosperms was held in India, including discussions of the positions of several critical families. Taken together, this literature has supported the view that embryological characteristics have a great deal to offer as sources of evidence for the systematics of higher-level groups among the flowering plants.

In this paper, we have analyzed the available information concerning the embryology of Myrtales and a few other families that have been thought to be closely related to this order. Our primary purpose has been to characterize Myrtales embryologically and to chart the main outlines of relationship within the order from an embryological perspective. As defined by Dahlgren and Thorne (1983), the families of core Myrtales are: Combretaceae, Crypteroniaceae, Lythraceae (including Punicaceae and Sonneratiaceae), Melastomataceae, Myrtaceae, Onagraceae, Oliniaceae, Penaeaceae, and Trapaceae. In addition, Chrysobalanaceae, Coridaceae, Elaeagnaceae, Elatinaceae, Haloragaceae, Lecythidaceae, Rhizophoraceae, Thymelaeaceae, which are excluded from the order by Dahlgren and Thorne (1983) but are "in various respects conspicuously similar to Myrtales," are analyzed from an embryological point of view in the light of the available information. We offer the present critical review to bring together all available literature and to serve as a guide to the most appropriate directions for future studies of the embryology of Myrtales.

Methods

In the course of this review we have analyzed nearly all of the references cited by Davis (1966), as well as the subsequent publications that have

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been available to us. Not all of these publications included information that was valuable for evaluating the embryology of Myrtales, and many had incomplete or inadequate information. For example, since the work of Geerts (1908) it has been understood that Onagraceae have the distinctive *Oenothera*-type embryo sac development. Earlier references such as those of Hofmeister (1847, 1858), Vesque (1879a, 1879b), Ward (1880), and Guignard (1882) were not able to explain this type of embryo sac development fully owing to the less precise techniques used in the nineteenth century (Maheshwari, 1948). Similarly, most other nineteenth-century embryological studies have relatively little to offer for current evaluations of the relationships of the families of angiosperms.

In general, only representative genera from individual families have been examined. The power of our comparisons between families is derived from the depth and scope of earlier investigations. We have attempted to take this factor into account in utilizing and evaluating the published information about the embryology of Myrtales and allied groups as follows:

$$\text{Level of knowledge (\%)} = \frac{\begin{array}{c}\text{Total number of}\\ \text{embryological studies}\\ \text{of anthers, ovules,}\\ \text{and seeds of genera}\\ \text{of a given family}\end{array}}{\begin{array}{c}3 \times (\text{number of}\\ \text{genera of the family})\end{array}} \times 100$$

We have divided the embryological data reviewed into three parts: namely, that concerning the anthers, ovules, and seed development. Most of the references we consulted refer to only one or two of these three major components of embryology. Comprehensive studies of all three classes of data provide the only sound basis for evaluating the relationships of genera and families. Even if some information is available, it may be strictly limited, and may therefore be of relatively little use. It is very rare, for example, for an earlier study to describe accurately the thickness of the integuments.

A second problem in utilizing published data concerning embryology concerns nomenclature. Names have sometimes changed so often in the past that it is difficult to be certain how many taxa are involved among those studied earlier. Except for Onagraceae and Penaeaceae, we have in general accepted the nomenclature used in the articles involved as a basic guide to the number of taxa studied earlier. For the number of genera in a given family, we have used Cronquist (1981) as a reference.

Despite these difficulties, we hope that our evaluation of the amount of knowledge available concerning the embryology of particular families will be useful in arriving at a sound understanding of the thoroughness of the earlier studies of the group and thus help the usefulness of the conclusions drawn for an evaluation of relationships.

EMBRYOLOGICAL CHARACTERS USED FOR ANALYSIS

The characters that are treated as most important in making these evaluations are basically those that Maheshwari (1964), Davis (1966), and Palser (1975) have considered "embryological characters of taxonomic significance." We have elected to use the whole set of characteristics so as to make what we believe to be the most effective comparison between families. Consequently, we have added several characters, such as thickness of integuments and presence or absence of fatty globules in megaspores of embryo sacs, to those treated as fundamental by the authors just mentioned. Specifically, we have dealt with the following 35 characters:

Anthers:

1. Number of sporangia per anther: four or more.
2. Type of wall development: Basic, Dicotyledonous, Monocotyledonous, Reduced.
3. Epidermis: persistent or not.
4. Endothecium develops fibrous thickenings or not.
5. Middle layers: persistent or not.
6. Tapetum: glandular or amoeboid.
7. Number of nuclei in a tapetal cell: one, two, or more.
8. Cytokinesis in a microspore mother cell: simultaneous or successive.
9. Shape of microspore tetrads: tetrahedral, decussate, isobilateral, or otherwise.
10. Number of cells in a mature pollen: one or two.

Ovules:

11. Degree of ovule curvature: anatropous, campylotropous, or otherwise.
12. Tenuinucellate or crassinucellate.
13. Number of integuments: one or two.

14. Thickness of integuments: two- or multi-layered.
15. Presence or absence of vascular tissue in integuments.
16. Micropyle: formed by inner, outer, or both integuments.
17. Nucellar beak formed or not.
18. Chalaza with hypostase or not.
19. Endothelium formed or not.
20. Archesporium one- or multi-celled.
21. Cytokinesis in a megaspore mother cell: occurs or not.
22. Shape of megaspore tetrads: linear, T-shaped, or otherwise.
23. Position of functional megaspore: micropylar or chalazal.
24. Type of megagametophyte development: *Polygonum, Oenothera, Penaea,* or other.
25. Fatty globules in megaspores and embryo sacs present or absent.
26. Characteristics of synergids: hooked, pyriform, or otherwise.
27. Characteristics of antipodal cells: persistent or ephemeral. Definitions of the term "persistent" and "ephemeral" were sometimes vague, so in this work the antipodal cells that degenerate and disappear before fertilization are referred to as "ephemeral," whereas those that persist up to fertilization and postfertilization are referred to as "persistent."
28. Number of constituent nuclei or cells in a mature embryo sac: eight (as is usual in the *Polygonum*-type embryo sac), five (due to early disintegration of three antipodal cells in the *Polygonum*-type embryo sac), four (as in the *Oenothera*-type sac), 16 (as in the *Penaea*-type embryo sac), or otherwise.

Seeds:

29. Path of pollen tube: porogamous, chalazogamous, or mesogamous.
30. Type of endosperm formation: nuclear or cellular.
31. Presence or absence of endosperm in mature seed.
32. Type of embryogeny: Onagrad, Solanad, Asterad, or otherwise.
33. Characteristics of suspensor: short, massive, haustorial, or otherwise.
34. Embryo with two equally developed cotyledons or not.
35. Polyembryony common or not.

Results and Discussion

Our results have been tabulated in order to facilitate comparisons among families (Tables 1–4). Of the families of interest, Crypteroniaceae (*Crypteronia, Axinandra,* and *Dactylocladus*), Chrysobalanaceae, and Coridaceae are unknown embryologically. In addition, many unusual and critical genera such as *Alzatea* and *Rhynchocalyx* (Lythraceae), *Strephonema* (Combretaceae), and *Psiloxylon* and *Heteropyxis* (Myrtaceae) are also unknown embryologically. The investigation of these taxa in relation to the characteristics presented in Tables 1–4 obviously is a matter of high priority.

Our embryological analyses, even though they were in most cases based on inadequate information, indicate clearly that many characteristics were consistent within given families (Table 1). Taken as a whole, they have made possible the definition of Myrtales as including a certain group of families linked together by their common possession of a set of shared embryological characteristics. This set of families agrees with that proposed as core Myrtales by Dahlgren and Thorne (1983): Combretaceae, Lythraceae (including Punicaceae and Sonneratiaceae), Melastomataceae, Myrtaceae, Onagraceae, Oliniaceae, Penaeaceae, and Trapaceae. The embryological characteristics common to this set of families are:

(1) Tapetum glandular (Table 2; Penaeaceae and Punicaceae are unknown in this respect).

(2) Ovule crassinucellate (Table 3).

(3) Inner integument two-layered (Table 3). The only known exception among the core families of Myrtales is *Syzygium* (Myrtaceae). Both in its initiation and subsequent early growth, the inner integument is consistently two-layered in all members of Myrtales except *Syzygium.* It forms a marked contrast with the outer integument, the thickness of which not only varies from genus to genus but which also tends to become thicker in the course of development. The analyses of Davis (1966, p. 15) indicated to her that the number of integuments present should be treated either as a generic or as a specific characteristic, but for Myrtales it appears to be of more fundamental significance. It seems clear that the unitegmic condition of the ovule in *Syzygium* must have originated secondarily within Myrtaceae; the distribution of this feature in the family should be studied further.

(4) Micropyle formed by both integuments

TABLE 1. General information and references of the embryology of Myrtalean and non-Myrtalean families analyzed.

Families	Number of Genera Studied So Far	Level of Knowledge	Selected References
Myrtales			
1. Combretaceae (20/400)	10	50%	Brewbaker (1967); Fagerlind (1941); Karsten (1891); Nagaraj (1954a, 1954b, 1954c, 1955); Pal (1951); Rao (1963); Venkateswarlu (1952b); Venkateswarlu and Rao (1972).
2. Lythraceae (23/500)	13	15%	Brewbaker (1967); Joshi and Venkateswarlu (1935a, 1935b); Smith and Herr (1971); Souèges (1925); Tischler (1917); Venkateswarlu (1937a); Warming (1878); Mauritzon (1934, 1939).
3. Melastomataceae (200/4,000)	19	3%	Brewbaker (1967); Crété (1956, 1957, 1960a, 1960b); Iconomides (1958); Ruys (1925); Subramanyam (1942, 1944, 1946, 1948, 1951); Ziegler (1925).
4. Myrtaceae (140/3,000)	29	9%	Brewbaker (1967); Davis (1968, 1969); Greco (1930); Mauritzon (1939); Narayanaswami and Roy (1960a, 1960b); van der Pijl (1934); Polunina (1957a, 1957b, 1957c, 1958a, 1958b, 1959, 1964); Prakash (1969a, 1969b, 1969c, 1969d, 1973); Roy (1953, 1955, 1960, 1961, 1962a, 1962b); Roy and Sahai (1962); Souèges (1940a); Tiwary and Rao (1934).
5. Oliniaceae (1/8)	1	66%	Mauritzon (1939).
6. Onagraceae (17/675)	12	37%	Beer (1905); Bonnet (1912); Brewbaker (1967); Gates (1911); Geerts (1908, 1909); Haberlandt (1927); Håkansson (1925); Hulbary and Rao (1959); Ishikawa (1918); Johansen (1928a, 1928b, 1929, 1930a, 1930b, 1931a, 1931b, 1931c, 1933, 1934); Kahn (1942); Lebègue (1948a, 1948b); Maheshwari and Gupta (1934); Modilewski (1909); O'Neal (1923); Pagni (1958); Renner (1914, 1921); Seshavataram (1967, 1970); Souèges (1920, 1935, 1946); Subramanyam and Govindu (1948); Täckholm (1914, 1915).
7. Penaeaceae (7/20)	4	38%	Stephens (1909).
8. Punicaceae (1/2)	1	33%	Brewbaker (1967); King (1947); Mauritzon (1939).
9. Sonneratiaceae (2/8)	2	83%	Joshi (1939); Karsten (1891); Mauritzon (1939); Venkateswarlu (1936a, 1936b, 1937b).

TABLE 1. (Continued).

Families	Number of Genera Studied So Far	Level of Knowledge	Selected References
10. Trapaceae (1/15)	1	100%	Brewbaker (1967); Ghosh (1954); Gibelli and Ferrero (1891); Ishikawa (1918); Ram (1956); Trela-Sawicka (1978).
Non-Myrtales			
11. Elaeagnaceae (3/50)	1	33%	Rau and Sharma (1970); Sharma (1966).
12. Elatinaceae (2/40)	2	83%	Dathan and Singh (1971); Frisendahl (1927); Kajale (1939); Lemesle (1929); Raghaven and Srinivasan (1940).
13. Haloragaceae (8/100)	3	38%	Bala-Bawa (1969a, 1969b, 1970); Brewbaker (1967); Kapil (1962); Kapil and Bala-Bawa (1968); Nagaraj and Nijalingappa (1967a, 1967b, 1974); Nijalingappa (1967); Souèges (1940b); Stolt (1928).
14. Lecythidaceae (20/400)	7	13%	Brewbaker (1967); Mauritzon (1939); Treub (1884); Venkateswarlu (1952a).
15. Rhizophoraceae (14/100)	6	12%	Brewbaker (1967); Carey (1934); Cook (1907); Juncosa (1982); Karsten (1891); Mauritzon (1939).
16. Thymelaeaceae (50/500)	18	17%	Brewbaker (1967); Fagerlind (1940); Fuchs (1938); Guérin (1913, 1915); Kausik (1940); Mauritzon (1939); Osawa (1913); Souèges (1942); Strasburger (1884); Venkateswarlu (1945, 1946, 1947a, 1947b); Vesque (1879a, 1879b); Winkler (1904).

(Table 3; except for the unitegmic *Syzygium*). According to Davis (1966, p. 16), in 88 of 189 families of angiosperms the micropyle is formed by the inner integument alone; in 74 families both integuments are involved; and in only four families is the micropyle formed by the outer integument. In the other families, the integumental components of the micropyle are constant within individual genera but vary from genus to genus within the family. These results suggest that variation in the participation of the inner and outer integuments in the formation of the micropyle is an important embryological characteristic with systematic significance. Within Myrtales, the cases of *Guiera senegalensis* (Combretaceae: Venkateswarlu & Rao, 1972), *Darwinia fascicularis* and *D. micropetala* (Myrtaceae; Prakash, 1969c), *Stenosiphon linifolius* (Onagraceae; Johansen, 1930b), in which the micropyle is apparently formed by the inner integument alone, should be regarded as isolated exceptions. In some of these instances, the formation of the micropyle is probably a secondary characteristic caused by the spatial condition of the ovarian locule (see footnotes 15 and 18 in Table 1). In *Trapa* (Trapaceae) the micropyle is not formed by integuments owing to the production of an elongated nucellar beak. The nucellar beak is evidently a secondary characteristic in angiosperms, and therefore its presence does not hinder the inclusion of Trapaceae in Myrtales.

(5) Antipodal cells absent or, if present, ephemeral (Table 3). Of the families of Myrtales

Table 2. Embryological data of anthers.

Families	Number of Sporangia	Anther Wall Development	Anther Epidermis	Endothecium	Middle Layers	Tapetum	Tapetal Cell	Cytokinesis in Meiosis	Microspore Tetrad	Mature Pollen Grain
Myrtales										
1. Combretaceae (20/400)	4	Basic type except in *Guiera senegalensis*	persistent (?)	fibrous	ephemeral	glandular	2-nucleate	simultaneous	tetrahedral or isobilateral	2-celled[1]
2. Lythraceae (23/500)	4	Dicotyledonous type[2]	—	fibrous[2]	ephemeral[2]	glandular[2]	2–6-nucleate[2]	simultaneous[2]	tetrahedral or isobilateral[2]	2-celled
3. Melastomataceae (200/4,000)	4	—	persistent	fibrous except in *Melastoma* and *Oxyspora*	ephemeral except in *Melastoma malabathricum*[3]	glandular	1-nucleate	simultaneous	tetrahedral	3-celled
4. Myrtaceae (140/3,000)	4	Basic type	persistent or ephemeral	fibrous	ephemeral	glandular	2-nucleate, but 1-nucleate in *Eucalyptus melliodora*	simultaneous	tetrahedral or decussate	2-celled
5. Oliniaceae (1/8)	4	—	—	fibrous (?)	ephemeral	glandular	2-nucleate (?)	—	—	—
6. Onagraceae (17/675)	4 or many[4]	—	persistent	fibrous	ephemeral	glandular	2-nucleate, but multinucleate in some species of *Oenothera* and *Fuchsia*	simultaneous	tetrahedral, isobilateral or decussate	2-celled
7. Penaeaceae (7/20)	—	—	—	—	—	—	—	—	—	—
8. Punicaceae (1/2)	—	—	—	—	—	—	—	—	—	2-celled
9. Sonneratiaceae (2/8)	4	Dicotyledonous type	persistent	fibrous	ephemeral	glandular	2-nucleate	—	—	2-celled

TABLE 2. (Continued).

Families	Number of Sporangia	Anther Wall Development	Anther Epidermis	Endothecium	Middle Layers	Tapetum	Tapetal Cell	Cytokinesis in Meiosis	Microspore Tetrad	Mature Pollen Grain
10. Trapaceae (1/15)	4	–	persistent	fibrous	ephemeral	glandular	multi-nucleate	simultaneous	tetrahedral or decussate	2-celled
Non-Myrtales										
11. Elaeagnaceae (3/50)	4	–	–	fibrous	ephemeral	glandular	2–4-nucleate	–	tetrahedral or decussate	3-celled
12. Elatinaceae (2/40)	4	Basic type	persistent	fibrous	ephemeral	glandular	2-nucleate in *Bergia* but 2–4-nucleate in *Elatine*	simultaneous	tetrahedral or isobilateral	2-celled in *Bergia*, but 3-celled in *Elatine*
13. Haloragaceae (8/100)	4	Monocotyledonous type	persistent	fibrous	ephemeral	glandular	1–5-nucleate	simultaneous	tetrahedral or decussate	3-celled
14. Lecythidaceae (20/400)	–	–	–	fibrous	ephemeral	amoeboid	2-nucleate	–	–	2-celled or 3-celled
15. Rhizophoraceae (14/100)	–	–	–	–	–	–	–	–	–	2-celled
16. Thymelaeaceae (50/500)	4	Monocotyledonous or Basic type	persistent	fibrous	ephemeral	glandular	2-nucleate, but 2–6-nucleate in *Wikstroemia*	simultaneous	tetrahedral or isobilateral	3-celled

[1] Pal (1951) reported the three-celled condition in *Terminalia catappa*, the only report which described this condition in Combretaceae. Other papers on *Terminalia catappa* (Nagaraj, 1954c; Venkateswarlu & Rao, 1972) and on other species of *Terminalia* (Nagaraj, 1954a; Venkateswarlu & Rao, 1972; Brewbaker, 1967) reported only the two-celled conditions.

[2] Based only on *Ammannia baccifera* (Joshi & Venkateswarlu, 1936).

[3] According to Subramanyam (1948), five to seven middle layers are formed in *Melastoma melabathricum*, the upper two or three persisting and the remainder ultimately crushed.

[4] *Calylophus, Clarkia, Gaura, Hauya, Heterogaura*, and two species of *Ludwigia* have polysporangiate anthers in which microsporogenous tissue is divided by sterile septa into many distinct packets (Raven, 1969; Eyde, 1978).

TABLE 3, part A. Embryological data of ovules. Abbreviations: i.i., inner integument; o.i., outer integument. See Table 3, part B, beginning on page 80, for additional characters; see page 82 for footnotes.

Families	Curvature[1]	Nature of Nucellus	Number of Integuments	Thickness of Integuments[2]	Vasculature of Integuments	Micropyle Formation	Nucellar Beak	Hypostase
Myrtales								
1. Combretaceae (20/400)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2-layered in most genera but 3-layered in *Terminalia* and *Bucida*	absent	i.i. and o.i. but only i.i. in *Guiera senegalensis*	not formed	present in some genera
2. Lythraceae (23/500)	anatropous	crassinucellate[8]	2	i.i. 2-layered; o.i. 2-layered in most genera but 5-layered in *Cuphea*	absent	i.i. and o.i.	not formed	absent except in *Ammannia*
3. Melastomataceae (200/4,000)	anatropous, or campylotropous (*Memecylon*)	crassinucellate	2	i.i. 2-layered; o.i. 2–3-layered	absent	i.i. and o.i.	not formed	absent
4. Myrtaceae (140/3,000)	anatropous	crassinucellate	2, but only 1 in *Syzygium*[9]	i.i. 2-layered; o.i. 2-layered in most genera but 2–4-layered in several genera	present in the single integument in *Syzygium*	i.i. and o.i. with a few exceptions[10]	not formed	present in some genera
5. Oliniaceae (1/8)	campylotropous	crassinucellate	2	i.i. 2-layered; o.i. 4-layered	present in o.i.	i.i. and o.i.	not formed	absent
6. Onagraceae (17/675)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2- or multi-layered	absent	i.i. and o.i., but i.i. in *Stenosiphon*[12]	not formed	present in most genera
7. Penaeaceae (7/20)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2-layered	absent	i.i. and o.i.	not formed	—
8. Punicaceae (1/2)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 4-layered	absent	i.i. and o.i.	not formed	absent

TABLE 3, part A, continued from page 78. Embryological data of ovules. Abbreviations: i.i., inner integument; o.i., outer integument. See Table 3, part B, beginning on page 80, for additional characters; see page 82 for footnotes.

Families	Curvature[1]	Nature of Nucellus	Number of Integuments	Thickness of Integuments[2]	Vasculature of Integuments	Micropyle Formation	Nucellar Beak	Hypostase
9. Sonneratiaceae (2/8)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2-layered	absent	i.i. and o.i.	not formed	absent
10. Trapaceae (1/15)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 5–14-layered	absent	not formed	formed	present
Non-Myrtales								
11. Elaeagnaceae (3/50)	anatropous	crassinucellate	2	—	—	—	not formed	present
12. Elatinaceae (2/40)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2-layered	absent	i.i. and o.i.	not formed	absent
13. Haloragaceae (8/100)	anatropous	crassinucellate	2	i.i. 2-layered; o.i. 2-layered	absent	i.i. and o.i.	not formed	present
14. Lecythidaceae (20/400)	anatropous	tenuinucellate	2	i.i. multi-layered; o.i. multi-layered	present in o.i.	i.i.	not formed	absent
15. Rhizophoraceae (14/100)	anatropous	crassinucellate	2	i.i. massive; o.i. massive	present in o.i. in some genera	i.i. and o.i. in *Bruguiera* and *Rhizophora*; only i.i. in *Gynotroches*; not formed in *Anisophyllea* (?)	formed in *Anisophyllea*	—
16. Thymelaeaceae (50/500)	anatropous	crassinucellate	2	i.i. 3–4-layered; o.i. 3–4- layered	absent	i.i.	not formed	present in many species

TABLE 3, part B. Embryological data of ovules. Abbreviations: i.i., inner integument; o.i., outer integument. See Table 3, part A, beginning on page 78, for additional characters; see page 82 for footnotes.

Families	Endothelium	Archesporium[3]	Cytokinesis in Meiosis	Megaspore Tetrad[4]	Functional Megaspore[5]	Pattern of Embryo Sac Formation	Fatty Globules in Megaspores and Embryo Sacs	Synergids	Antipodal Cells	Number of Nuclei in Mature Embryo Sac
Myrtales										
1. Combretaceae (20/400)	not formed	1-celled[6]	occurs	linear	chalazal cell	*Polygonum* type[7]	absent	hooked and pyriform	ephemeral, but persistent in *Guiera senegalensis*	5, but 8 or more in *Guiera senegalensis*
2. Lythraceae (23/500)	not formed	multi-celled; only one functions	occurs	linear	chalazal cell	*Polygonum* type	absent	hooked	ephemeral	5
3. Melastomataceae (200/4,000)	not formed	1-celled	occurs	linear	chalazal cell	*Polygonum* type	absent	hooked	ephemeral	5
4. Myrtaceae (140/3,000)	not formed[11]	1-celled	occurs	linear	chalazal cell	*Polygonum* type	absent, but present in *Psidium guajava*	diverse in form	ephemeral	5
5. Oliniaceae (1/8)	not formed	1-celled	occurs	linear	chalazal cell	*Polygonum* type	absent	—	ephemeral	5
6. Onagraceae (17/675)	not formed	1-celled	occurs	linear	micropylar cell	*Oenothera* type	absent	filiform	absent	4
7. Penaeaceae (7/20)	not formed	1-celled	does not occur	decussate[13]	all 4 nuclei	*Penaea* type	absent	—	absent	16
8. Punicaceae (1/2)	not formed	1-celled	occurs	linear	chalazal cell	*Polygonum* type	absent	elongated	ephemeral	5
9. Sonneratiaceae (2/8)	not formed	multi-celled; only one functions	occurs	linear	chalazal cell	*Polygonum* type	present in *Sonneratia* but absent in *Duabanga*	hooked	ephemeral	5

TABLE 3. part B, continued from page 80. Embryological data of ovules. Abbreviations: i.i., inner integument; o.i., outer integument. See Table 3, part A, beginning on page 79, for additional characters; see page 82 for footnotes.

Families	Endothelium	Archesporium[3]	Cytokinesis in Meiosis	Megaspore Tetrad[4]	Functional Megaspore[5]	Pattern of Embryo Sac Formation	Fatty Globules in Megaspores and Embryo Sacs	Synergids	Antipodal Cells	Number of Nuclei in Mature Embryo Sac
10. Trapaceae (1/15)	not formed	1–2-celled	occurs	linear	chalazal cell	*Polygonum* type	absent	pyriform	ephemeral	5
Non-Myrtales										
11. Elaeagnaceae (3/50)	–	1–3-celled	occurs	linear	chalazal cell	*Polygonum* type	absent	–	ephemeral	5
12. Elatinaceae (2/40)	not formed	multi-celled; only one functions	occurs	linear or T-shaped	chalazal cell	*Polygonum* type	absent	hooked and pyriform in *Bergia ammanioides*	ephemeral	8
13. Haloragaceae (8/100)	not formed	1-celled	occurs	linear	chalazal cell	*Polygonum* type	absent	hooked and pyriform	persistent	8
14. Lecythidaceae (20/400)	formed in many species[14]	multi-celled; only one functions	occurs	linear	chalazal cell	*Polygonum* type	absent	pyriform	ephemeral	5
15. Rhizophoraceae (14/100)	formed in *Carallia, Gynotroches, Bruguiera* and *Cassipourea*	1-celled	occurs	linear	chalazal cell	*Polygonum* type	absent	pyriform	ephemeral in *Ceriops* but persistent in *Gynotroches*	5 or 8
16. Thymelaeaceae (50/500)	not formed	1-celled	occurs	linear	chalazal cell	*Polygonum* type	absent	hooked, rarely filiform (*Daphne cannabina*)	persistent; cells usually amplify (up to as many as 30 in *Thymelaea arvensis*)	8 or more

TABLE 3, parts A & B, concluded. Footnotes.

[1] Predominant or usual condition.

[2] Based on the original thickness of integuments seen at the initiation and early growing stage.

[3] Predominant or usual condition.

[4] Predominant or usual condition.

[5] Predominant or usual condition.

[6] Venkateswarlu (1952) described that a multi-celled archesporium was common in *Poivrea coccinea* (= *Combretum coccinea*), and Nagaraj (1954c, 1955) also reported the common occurrence of a multi-celled archesporium in *Terminalia catappa* and *T. belerica*. Therefore, Davis (1966, p. 87) described that "commonly several archesporial cells differentiate" in Combretaceae. In contrast, other more recent papers by Rao (1963) and by Venkateswarlu and Rao (1972), the latter of which dealt with 18 species in 9 genera (including *Terminalia* and *Combretum*), made it clear that the one-celled archesporium is common and the multi-celled one (i.e., consisting of two or more cells) is rare.

[7] Mauritzon (1939) reported the 16-nucleate *Penaea*-type embryo sac in two species of *Combretum*, *C. paniculatum* and *C. pincianum*. These results need to be reconfirmed because other authors have reported only *Polygonum*-type embryo sacs in *Combretum*. Variation in female gametophyte formation is known in some genera, however (see Hjelmquist, 1964), for review.

[8] Smith and Herr (1971, p. 198), contrary to many other authors, stated that "the nucellus of *Ammannia coccinea* was tenuinucellate." But tenuinucellate ovules have never been reported in other species of *Ammania* nor in other Lythraceae. The drawings of sections of ovules (Smith & Herr, 1971, p. 167, Figs. 4 and 5) which they intended to document the existence of tenuinucellate condition of this species indicate rather that their material was clearly crassinucellate: the subhypodermal cells that they identified with the archesporial cells are evidently megaspore mother cells cut off from the actual archesporial cells.

[9] Besides the species of *Syzygium*, *Eugenia paniculata* (Mauritzon, 1939), *E. jambos* (Pijl, 1934), *E. malaccensis* (Pijl, 1934; Roy, 1960), *E. fruticosa* (Roy, 1961) and *E. myrtifolia* (Roy, 1962b) are reported to have a unitegmic ovule. But all of these *Eugenia* are assigned to *Syzygium* (sensu Schmid, 1972): according to Schmid (pers. comm.), *Eugenia paniculata* is assigned to *Syzygium paniculatum* Gaertner, *Eugenia jambos* to *Syzygium jambos* (L.) Alston, *Eugenia malaccensis* to *Syzygium malaccense* (L.) Merr. & Perry, *Eugenia fruticosa* to *Syzygium fruticosum* DC., and *Eugenia myrtifolia* to *Syzygium myrtifolium* (Roxb.) DC. On the other hand, *Eugenia bracteata*, which should remain in *Eugenia* sens. str. sensu Schmid, has a bitegmic ovule (Roy, 1955).

[10] Mauritzon (1939, p. 110) states that "it appears that it is not unusual in the Myrtaceae for the micropyle to be formed entirely or mainly by the inner integument." In fact, *Darwinia fascicularis* and *D. micropetala* have the micropyle formed by the inner integument alone (Prakash, 1969c), whereas *Darwinia taxifolia* has one formed by both integuments (Mauritzon, 1939). Thus there is variation even within the genus *Darwinia* in the participation of integuments in the formation of the micropyle. The secondary growth of the inner integument combined with the suppression of growth of the outer integument because of the limited space available within the ovarian locule may result in the formation of the micropyle by the inner integument only. In both species of *Darwinia* that have the micropyle formed by the inner integument only, the inner integument develops into "collar-like lips" (Prakash, 1969c), a condition that clearly seems to be secondary.

[11] Endothelium has not been reported in references, but in *Leptospermum*, *Kuntzea*, *Agonis*, *Callistemon*, and *Melaleuca*, the upper part of the nucellus tends to be destroyed by the growth of the embryo sac, a feature that would normally accompany the development of an endothelium. In *Melaleuca* particularly, the mature embryo sac borders directly on the inner integument (Mauritzon, 1939).

[12] In *Stenosiphon linifolius* the micropyle is formed by the extremely elongated "beak-like process" of the inner integument (Johansen, 1930b) a characteristic that seems to be secondary in the family.

[13] Cell walls are absent, but four megaspore nuclei are arranged in such a way that one lies at the top, one lies at the bottom, and the other two lie at the sides. The decussate arrangement is acquired by oblique divisions of the micropylar nucleus and of the chalazal nucleus that were formed by meiosis I, and not by a combination of vertical and transverse divisions.

[14] According to Mauritzon (1939), an endothelium (called a "mantle layer" by him) is formed in *Couroupita guianensis*, *Careya arborea*, and *Barringtonia speciosa* but not in other species of *Barringtonia* nor in *Gustavia angusta*. Venkateswarlu (1952) reported its occurrence both in *Napoleona imperialis* and in *Barringtonia acutangula*. The absence of an endothelium in some species of *Barringtonia* and *Gustavia* should be reconfirmed, because the presence of endothelium is otherwise a family characteristic of Lecythidaceae (Davis, 1966, p. 16). Probably Mauritzon's observations had not extended to old enough stages of ovule development to observe the endothelium and it is likely that it is present in all members of Lecythidaceae.

mentioned above, all except Onagraceae and Penaeaceae consistently have ephemeral antipodal cells that degenerate and disappear before fertilization. In these families, therefore, the mature embryo sac comprises only five nuclei or cells: an egg; two synergids; and two polar nuclei, which may fuse into a secondary nucleus before fertilization. This relationship suggests that for Myrtales the antipodal cells are unnecessary in the organized mature embryo sac. Exceptionally, the antipodal cells of *Guiera senegalensis* (Combretaceae) persist into the postfertilization phase, a feature that is regarded as unique for Combretaceae (Venkateswarlu & Rao, 1972). In Onagraceae and Penaeaceae, antipodal cells are absent throughout megagametophyte development. In the 16-nucleate *Penaea*-type embryo sac, one might regard the three chalazal cells as corresponding to the antipodal cells. Stephens (1909) mentioned, however, that these three chalazal cells resembled an egg apparatus more or less closely. In fact, the three chalazal cells are produced in the same way as the three cells of a true micropylar egg apparatus, but from a different megaspore nucleus.

(6) Nuclear-type endosperm formation (Table 4).

(7) Exalbuminous seed (Table 4).

Core Myrtales

Taken together, these features characterize the core Myrtales group defined by Dahlgren and Thorne (1983). Within this assemblage, Lythraceae are further characterized (except for *Punica*) by having a multi-celled archesporium in the ovule, a feature that is not common elsewhere in the order. Although this characteristic has in general received less attention than other embryological features, it does appear to have some value at least in particular cases. Thus, Vijayaraghavan (1970) adopted it as one of the bases for the exclusion of *Paeonia* from Ranunculaceae.

Sonneratia and *Duabanga*, usually taken as constituting a separate family Sonneratiaceae, agree with other Lythraceae in having a multi-celled archesporium. Embryologists as well as other students of plant systematics have in general argued for a close relationship among these groups (Joshi, 1939; Venkateswarlu, 1936a, 1936b, 1937b). In agreement with these observations, our analysis of the embryological literature offers no basis for distinguishing between them, and supports their inclusion in a single family (Dahlgren & Thorne, 1983). *Sonneratia* and *Duabanga* differ in that the former consistently has fatty globules in its megaspores and embryo sacs whereas these are lacking in *Duabanga* (Karsten, 1891; Venkateswarlu, 1937b; Mauritzon, 1939). This accords with certain other lines of evidence in suggesting that these genera may not be directly related to one another.

Punica differs from other Lythraceae in having a uni-celled archesporium, and a thick multi-layered outer integument. Nonetheless, it is included in Lythraceae by Dahlgren and Thorne (1983). Further embryological studies on *Punica* are clearly needed.

Although many of the embryological characteristics of Penaeaceae are unknown, those that have been investigated clearly warrant inclusion of this unusual South African family in Myrtales. The only distinctive feature among those that have been reported is the characteristic 16-nucleate *Penaea*-type embryo sac. This type of embryo sac development is characterized by the fact that meiosis in the megaspore mother cell is not accompanied by cytokinesis. Following meiosis, all four of the decussately arranged megaspore nuclei function, each dividing twice to produce four nuclei or cells. The quartet associated with the true micropylar egg apparatus is always derived from the micropylar megaspore nucleus (Stephens, 1909). In both the frequency of division of the megaspore nucleus and the origin of the egg apparatus, the *Penaea*-type embryo sac development resembles the *Oenothera*-type of embryo sac development that is characteristic of Onagraceae, discussed below (see also Maheshwari, 1948).

Melastomataceae exhibit a distinctive embryological feature that is unknown elsewhere in the order, uni-nucleate anther tapetum cells in place of the bi- or multi-nucleate ones characteristic of other families of Myrtales. In addition, Melastomataceae are the only family of Myrtales in which the endothecium sometimes develops fibrous thickenings. Another distinctive feature that has been claimed for Melastomataceae is three-celled mature pollen, in place of the two-celled mature pollen characteristic of all other families of Myrtales. A careful review of the few published reports, however, has indicated that Melastomataceae, like all other core Myrtales, have two-celled mature pollen (Tobe & Raven, in prep.). In this connection, it seems to be worthwhile to note the fact that the pollen cell con-

TABLE 4. Embryological data of seeds.

Families	Path of Pollen Tube	Endosperm Formation	Endosperm in Mature Seed	Embryogeny	Suspensor	Embryo	Polyembryony
Myrtales							
1. Combretaceae (20/400)	porogamous	Nuclear type	absent	Asterad type	short and small	2 cotyledons with same size	rare
2. Lythraceae (23/500)	porogamous	Nuclear type	absent[1]	Onagrad type[1]	short and small[1]	2 cotyledons with same size	absent
3. Melastomataceae (200/4,000)	porogamous	Nuclear type	absent	Onagrad type	short and massive	2 cotyledons with same size	occasional
4. Myrtaceae (140/3,000)	porogamous	Nuclear type	absent	Onagrad type	short and small, or absent	2 cotyledons with same size	usual in *Syzygium*
5. Oliniaceae (1/8)	–	Nuclear type	–	–	–	–	–
6. Onagraceae (17/675)	porogamous	Nuclear type	absent	Onagrad type	short and small	2 cotyledons with same size	rare
7. Penaeaceae (7/20)	porogamous	Nuclear type	absent	Asterad type	absent	2 cotyledons with same size	–
8. Punicaceae (2/8)	–	Nuclear type	–	–	–	–	–
9. Sonneratiaceae (2/8)	porogamous	Nuclear type	absent	Onagrad type	short and small	2 cotyledons with same size	absent
10. Trapaceae (1/15)	porogamous	Nuclear type	absent	Solanad type	long, coiled, haustorial; the upper part forming collar	2 cotyledons with extremely different size	absent

TABLE 4. *(Continued).*

Families	Path of Pollen Tube	Endosperm Formation	Endosperm in Mature Seed	Embryogeny	Suspensor	Embryo	Polyembryony
Non-Myrtales							
11. Elaeagnaceae (3/50)	–	Nuclear type	absent	Asterad type	short and massive	2 cotyledons with same size	absent
12. Elatinaceae (2/40)	–	Nuclear type	present	Solanad type	short and small	2 cotyledons with same size	absent
13. Haloragaceae (8/100)	porogamous	Nuclear type in *Laurembergia* but Cellular type in *Haloragis* and *Myriophyllum*[2]	present	Caryophyllad type	2-celled, enlarged, haustorial	2 cotyledons with same size	absent
14. Lecythidaceae (20/400)	–	Nuclear type	–	–	short and massive in *Barringtonia vriesei*	–	–
15. Rhizophoraceae (14/100)	porogamous	Nuclear type	present	–	short and massive, or long	2 cotyledons with same size	rare
16. Thymelaeaceae (50/500)	porogamous	Nuclear type	present[3]	Asterad type	short and small, or absent	2 cotyledons with same size	rare

[1] Based only on *Duabanga sonneratioides* (Venkateswarlu, 1937b).

[2] Even in the Nuclear type, cell wall formation commences as early as the 8-nucleate stage (Bala-Bawa, 1969a; Nagaraj & Nijalingappa, 1974), a phenomenon that demonstrates a strong tendency towards the Cellular type.

[3] According to Guérin (1915), in Thymelaeaceae seeds that completely lack endosperm are rather exceptional. Even in the species of *Phaleria* which nearly lack endosperm, two- to five-layered endosperm tissue was present on the surface of the cotyledons in the mature seed.

dition is highly consistent in the order (cf. Brewbaker, 1967). The pollen cell condition of Melastomataceae should be studied further.

Although little is known about the embryology of Oliniaceae, what is known clearly supports their inclusion within Myrtales, as do their other features (Rao & Dahlgren, 1969). The only known distinctive feature is the thick, vascularized outer integument. Closer comparisons with Melastomataceae ought to be made when more information is available, following the suggestions of Rao and Dahlgren (1969); the comparisons with Thymelaeaceae and Rubiaceae suggested by these authors cannot be taken as indications of genuine relationship in view of the embryological and other features of *Olinia*.

Combretaceae have been studied as extensively from an embryological point of view as any family of Myrtales. *Guiera* differs in several respects from the other members of the family and indeed stands out within Myrtales, but in general, Combretaceae agree closely in their embryological features with other Myrtales. *Guiera* differs from all other Myrtales in having persistent antipodal cells and a micropyle formed by the inner integument only (Venkateswarlu & Rao, 1972). Based on these features, Venkateswarlu and Rao (1972), taking into account also evidence from floral morphology and anatomy, proposed the establishment of a unigeneric tribe, Guiereae, for *Guiera*. In its overall features, however, *Guiera* clearly fits into the subtribe Combretinae together with *Combretum* and other genera (Stace, 1965; Exell & Stace, 1966, 1972), so that its unusual embryological attributes must almost certainly be secondary. The persistence of antipodal cells, which multiply after fertilization, seems clearly to be secondary, and it appears logical to consider the lack of participation of the outer integument in the formation of the micropyle secondary also.

From an embryological point of view, Trapaceae are the most distinctive family included in Myrtales. A long nucellar beak is formed in *Trapa* as a result of an extension of the apex of the nucellus. The formation of this beak evidently precludes direct participation of the integuments in the formation of the micropyle. A second very distinctive feature of *Trapa* is the long, coiled haustorial suspensor, the upper part of which forms a collar supporting the embryo proper. A third distinctive feature is the asymmetrical embryo, which has two very unequal cotyledons. Some or all of these features might be related to the aquatic habitat of the family but this suggestion needs further evaluation. Other embryological characteristics of this monogeneric family include the thick, nonvascularized outer integument and the multinucleate anther tapetal cells. The embryological characteristics of Trapaceae do not support a direct relationship either with Onagraceae (a family in which Trapaceae were formerly included) or with Lythraceae (contrary to the views of Miki, 1959).

Myrtaceae, like Combretaceae, have few distinctive features that discriminate them from other Myrtales. *Syzygium* is unique in the order in its unitegmic ovules. Doubtless this represents a derived feature as it does in angiosperms generally (Bouman, 1977), and it probably will be found in other genera when the family is better known embryologically. Mauritzon (1939, p. 102–103) stated that in "*Eugenia paniculata*" (=*Syzygium paniculatum*) "two two-layered integuments have fused together to form a single integument of four layers." Unitegmy could also be derived by the loss of one of the two integuments. A third way in which unitegmy could be derived has recently been suggested by Bouman (1977) and Bouman and Schier (1979). These authors have concluded that both in Ranunculaceae and in Gentianaceae unitegmy has originated following a complicated process involving the fusion of the primordia that has led to a shifting of the inner integument and an arrested development of it subsequently. If unitegmy has originated in this way in *Syzygium*, a major part of its single integument would be composed of the outer integument. This integument might then represent an ancestral form of outer integument in Myrtaceae, as suggested by its thickness and possession of a vascular supply. Regardless of the exact method of derivation however it appears virtually certain that unitegmy in *Syzygium* has been derived from bitegmy within Myrtaceae because the genus is not otherwise remarkable within the family. The distribution of unitegmy in Myrtaceae should be investigated further.

Onagraceae are characterized by their distinctive 4-nucleate *Oenothera*-type embryo sac, unknown elsewhere in angiosperms. This family has been considered to have a close relationship to Lythraceae, and several embryologists such as Tischler (1917), Mauritzon (1934), and Joshi and Venkateswarlu (1936) considered that the Lythraceous embryo sac with ephemeral antipodal cells forms phylogenetically an intermediate stage

between the 4-nucleate embryo sac of Onagraceae and the normal 8-nucleate embryo sac. In fact, ephemeral antipodal cells are common to most members of the order Myrtales, and the condition in Lythraceae cannot, therefore, be taken as indicative of a direct relationship between this family and Onagraceae. The Onagrad-type embryogeny common to both families occurs in Myrtaceae and Melastomataceae as well. Thus none of the embryological attributes of Onagraceae suggests a particular relationship either to Lythraceae or to any other family. Embryologically, the relationship between the 4-nucleate *Oenothera*-type of embryo sac in Onagraceae and the 16-nucleate *Penaea*-type embryo sac in Penaeaceae appears to be of more interest, and perhaps more suggestive of a direct relationship. These types of embryo sac development resemble one another in that antipodal cells are not formed at all during megagametogenesis and also in that the micropylar megaspore nucleus in both families divides only twice to form an egg apparatus (see also Maheshwari, 1948). Although these similarities may have originated as a result of convergent evolution, they do at least indicate that the loss of the antipodal cells by omission of the third nuclear division in megagametogenesis has occurred twice in Myrtales, since Penaeaceae and Onagraceae are manifestly not related directly to one another. At present, we suggest that ephemeral antipodal cells constitute a primitive condition in Myrtales that was present in the common ancestor.

Evaluation of Other Families

Among the families that have been thought to be related to or possibly included within Myrtales, we shall discuss first Haloragaceae. Haloragaceae share with the core Myrtales the following features: glandular tapetum; crassinucellate ovule; 2-layered inner integument; and micropyle formed by both integuments. Haloragaceae differ fundamentally from Myrtales, however, in having (1) persistent antipodal cells; (2) either Cellular- or Nuclear-type endosperm formation (Nuclear-type endosperm formation in Haloragaceae when present closely resembles the Cellular-type endosperm formation); (3) albuminous seeds. In addition, Haloragaceae differ from core Myrtales in exhibiting the Monocotyledonous-type of anther wall formation; Caryophyllad-type embryogeny; and a 2-celled, enlarged haustorial suspensor. This type of haustorial suspensor may be related to the adaptation of Haloragaceae to a more or less aquatic habitat. In this connection it may be noted that Trapaceae, which are also strictly aquatic, also have a very distinctive type of haustorial suspensor. Taken together, these embryological features virtually exclude the possibility of any direct relationship of Haloragaceae with Myrtales.

Insufficient information concerning Rhizophoraceae (including Anisophylleaceae) is available to characterize the family or its constituent parts. Notwithstanding this, in their massive inner integument and albuminous seeds, Rhizophoraceae differ sharply from Myrtales. The available embryological information indicates a considerable heterogeneity within the family and might be taken to support the contention that it should be divided into two or more families, which might not be related directly to one another. In *Bruguiera* and *Rhizophora* (Rhizophoreae) the micropyle is formed by both integuments (Cook, 1907; Carey, 1934; Mauritzon, 1939), and in *Gynotroches* (Gynotrocheae) it is formed by the inner integument alone (Mauritzon, 1939). In *Anisophyllea* (Anisophylleeae) the extension of the nucellar apical tissue (? = nucellar beak) prevents the formation of the micropyle by integuments (Karsten, 1891). Furthermore, an endothelium is formed in *Carallia* and *Gynotroches* (Gynotrocheae; Karsten, 1891; Mauritzon, 1939), *Cassipourea* (Macarisieae; Juncosa, 1982) and in *Bruguiera* (Rhizophoreae; Mauritzon, 1939) but not in the other genera. The antipodal cells are ephemeral in *Ceriops* and *Bruguiera* (Rhizophoreae) but persistent in *Gynotroches* (Gynotrocheae; Karsten, 1891; Mauritzon, 1939). The outer integument is vascularized in *Rhizophora, Ceriops,* and *Bruguiera* (Rhizophoreae; Carey, 1934; Mauritzon, 1939), but probably not in the other tribes. The endothelium and the nature of the integuments that form the micropyle appear to be characteristic of Rhizophoraceae at the family level (Davis, 1966). Those members of Rhizophoraceae with persistent antipodal cells differ from Myrtales in this respect. Further detailed study on the embryology of the various genera of Rhizophoraceae should be valuable in evaluating the apparent heterogeneity of this family.

Thymelaeaceae differ from Myrtales in possessing (1) a thick, 3- to 4-layered inner integument; (2) micropyle formed by the inner integument alone; (3) persistent antipodal cells that often multiply; and (4) albuminous seeds. Em-

bryologically, these differences are decisive in ruling out any direct relationship between Thymelaeaceae and core Myrtales.

Lecythidaceae have many distinctive features embryologically. They are: (1) an amoeboid anther tapetum; (2) tenuinucellate ovule; (3) a thick, multi-layered inner integument; and (4) micropyle formed by the inner integument alone. In addition, the family is characterized by having an endothelium (Mauritzon, 1939). This combination of features seems decisive in precluding any direct relationship between Lecythidaceae and Myrtales.

Although its two constituent genera differ in several respects, Elatinaceae agree with Myrtales in many embryological features. Among them are the glandular anther tapetum; crassinucellate ovule; a 2-layered inner integument; a micropyle formed by both integuments; ephemeral antipodal cells; and Nuclear-type endosperm formation. The only known embryological difference between Elatinaceae and Myrtales concerns the albuminous seeds of Elatinaceae compared with the exalbuminous seeds of Myrtales. Frisendahl (1927) observed a one-layered endosperm in ripe seeds of *Elatine* spp. Dathan and Singh (1971) observed a three- to five-layered endosperm in mature seeds of both *Bergia odorata* and *B. ammanioides* and a one- to two-layered one in those of *B. aestivosa*; in contrast, Raghaven and Srinivasan (1940) did not observe endosperm in the mature seeds of *Bergia capensis*.

Despite the difference in persistence of endosperm, on the basis of embryological features alone we would suggest that Elatinaceae might be placed adjacent to core Myrtales. The classifications of Takhtajan (1980) and Cronquist (1981) regard Elatinaceae as having a close relationship with Clusiaceae-Hypericoideae. Embryologically, Hypericoideae differ markedly from Elatinaceae in having tenuinucellate ovules and an endothelium, and we suggest that this relationship suggested by Takhtajan and Cronquist is probably incorrect.

Elaeagnaceae have been studied very inadequately from an embryological point of view. Not enough information is available, particularly concerning the integuments, to evaluate properly the possibility of a relationship between the Elaeagnaceae and Myrtales on that basis. Available information indicates that Elaeagnaceae share the following embryological features with Myrtales, however: glandular anther tapetum; crassinucellate ovule; ephemeral antipodal cells; Nuclear-type endosperm formation; and exalbuminous seeds. The embryology of Elaeagnaceae should be studied in more detail and the possibility of a relationship of this family with Myrtales should be evaluated further in the light of this information.

In summary, Myrtales are clearly circumscribed by embryological evidence to include Combretaceae, Lythraceae (including Punicaceae and Sonneratiaceae), Melastomataceae, Myrtaceae, Onagraceae, Oliniaceae, Penaeaceae, and Trapaceae. We further suggest that the possibility of a direct relationship between Elatinaceae and Myrtales is supported by embryological data and should be investigated further from a number of other points of view.

Within Myrtales, the large families Myrtaceae and Combretaceae seem not to be distinctive and to agree with the generalized characteristics of the order in their embryological features. Lythraceae (including Punicaceae and Sonneratiaceae) seem to form another relatively generalized group within the order, standing apart somewhat from Myrtaceae and Combretaceae in their multi-celled archesporium. This multi-celled archesporium might be taken either as a secondary or as a primary characteristic, and its nature should be investigated further in the context of phylogenetic studies of the group. Melastomataceae deviate from all other families of Myrtales in the characteristics of their anthers. Penaeaceae and Onagraceae, although the latter are much more generalized than the former in their embryological characteristics, are both relatively specialized in their loss of antipodal cells. Three small families of Myrtales that otherwise seem not to be directly related to one another—Oliniaceae, Punicaceae (included by Dahlgren & Thorne, 1983, in Lythraceae), and Trapaceae—share with one another a thick, multi-layered outer integument. Students who have recently considered the evolution of integuments, especially Bouman and his colleagues, have generally considered that the evolutionary trend in the integuments of angiosperms proceeds from a thick to a thin integument (see Boesewinkel, 1981). If this relationship is accepted, then it would be assumed that Oliniaceae, Punicaceae, and Trapaceae may retain the primitive integumental condition for Myrtales. In that case, Punicaceae although they might still legitimately be regarded as belonging in Lythraceae, might be viewed as a distinctive, archaic offshoot within that family.

Trapaceae are more distinctive in their embryology than any other family of Myrtales and differ more from the core Myrtales in their embryological features than do Elatinaceae.

Future Directions for Research

More embryological information about Myrtales should prove useful in elucidating further the relationships of the families of the order in the future, and in turn in evaluating the relationships of this order to other groups of angiosperms. Even though the available embryological evidence has allowed a clear circumscription of Myrtales on embryological grounds alone, our comparisons of many taxa are based on incomplete information. It is particularly critical that no information at all has been available on a number of very interesting genera of Myrtales such as: *Alzatea, Axinandra, Crypteronia, Dactylocladus,* and *Rhynchocalyx,* one, several, or all of which may constitute Crypteroniaceae (Van Beusekom-Osinga & Van Beusekom, 1975; van Vliet, 1975; van Vliet & Baas, 1975; Muller, 1975; Cronquist, 1981; Dahlgren & Thorne, 1983). It is likewise unfortunate that no information has been available on *Strephonema,* a very distinctive genus in Combretaceae (Dahlgren & Thorne, 1983). Only a little information is available on *Heteropyxis* and *Psiloxylon,* genera that might be regarded as constituting distinct families or be included within Myrtaceae depending upon one's point of view (Schmid, 1980). Even though all of these genera clearly belong within the order Myrtales, a study of their embryology has the potential of contributing much to our overall understanding of the elements within this order.

In addition, Oliniaceae, Penaeaceae, and Punicaceae are poorly known embryologically, and more information is necessary for a proper evaluation of their status and relationships. Even Melastomataceae and Myrtaceae, for which the level of knowledge from an embryological point of view was estimated as only 3% and 9% respectively, should be studied more extensively. Since these are the two largest families of the order, an examination of their embryological attributes is critical.

Among the groups that have been included within or said to be related to Myrtales, no detailed embryological information is available concerning Chrysobalanaceae and Coridaceae. Chrysobalanaceae are sometimes considered to be closely allied to the ancestor of Myrtales because of their possession of many common features (Dahlgren & Thorne, 1983). Dahlgren and Thorne (1983) indicated a few gross embryological features of these families including the fact that in Chrysobalanaceae the ripe seeds are exalbuminous, and in Coridaceae, the ovules are bitegmic and tenuinucellate. As regards Rhizophoraceae, embryological evidence suggests a considerable degree of heterogeneity, which accords with the conclusions of Dahlgren and Thorne (1983) and others about the basic heterogeneity of the family. Detailed information about the embryology of the constituent parts of Rhizophoraceae *sens. lat.* would no doubt contribute in an important manner to the resolution of the problem of relationships of Rhizophoraceae and the proper constituency of this family.

A few comments on the references we consulted during the course of preparation of this paper are now appropriate. Most of these references were incomplete, even though the respective authors might have drawn a great deal more from the materials that they had available at the time they conducted their studies. Traditionally, embryological studies have been directed much more closely to the development of the gametophyte than to other features of great systematic interest such as the development of the nucellus and that of the integuments. As mentioned above, very few studies refer to the thickness of the integuments except in descriptions of the structure of seed coats. Despite this, a proper understanding of the thickness of the integuments seems clearly to be of some value as an indicator of affinity and phylogenetic advancement of respective groups. The thickness of secondarily amplified integuments seems to be of less interest as a systematic characteristic than is the original thickness as the integuments are initiated and starting to grow. The thickness of mature integuments is directly related to the structure of the mature seed coats, which may be highly diverse even within a single genus or a group of related genera; e.g., "*Eucalyptus*" (Gauba & Pryor, 1958, 1959, 1961). More information about the thickness of the integuments and their structure before they begin to thicken during the course of seed coat formation will probably prove to have considerable significance for systematic comparisons. In this connection, Bouman (1971, p. 175) stated that "seemingly identical multi-layered integuments (such as those of Juglandaceae and Liliiflorae) originate by means of different on-

togenetic processes" and that "characters derived from the structure of mature seed coats are of doubtful taxonomic significance at and above the family level, unless they are amplified by developmental studies." We believe that integumentary studies combined with those of histogenesis should be incorporated routinely into embryological studies, particularly those intended to have systematic application.

Many embryological studies are devoted to abnormal or exceptional cases, and there is less attention generally given to those characteristic features for particular groups that may have much greater taxonomic importance. In many references, it is difficult or impossible to determine which was the characteristic state for the taxon being investigated. Thus, the archesporium may be described as one- to three-celled or as one-celled but occasionally multi-celled, but without any explanation as to which was the characteristic state for that taxon. Exact statements about the proportions in which these different states were represented will be important for a proper evaluation of embryological reports and for promoting their utility in the future. Similar observations could be applied to reports of the characteristics of megaspore tetrads, functional megaspores, the number of nuclei in tapetal cells, and of microspore tetrads. Thus we would conclude that embryological studies should be more extensive in respect of the features that they consider and report, and more precise in terms of the way in which they handle anomalous or exceptional situations encountered.

In conclusion, embryological features afford a sound basis for the delineation of Myrtales. There are, however, many gaps to be filled in our knowledge of the taxa that clearly belong within this order, and other taxa that may or may not be directly related to it. A careful choice of the characters to be examined and critical descriptions of these characteristics will assist greatly in our ongoing evaluation of relationships within Myrtales and allied groups.

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REVISION OF THE ARBORESCENT BAUHINIAS (FABACEAE: CAESALPINIOIDEAE: CERCIDEAE) NATIVE TO MIDDLE AMERICA[1]

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Abstract

Twenty-seven arborescent species of *Bauhinia* native to Middle America, of which 20 species are endemic, are recognized in a systematic treatment. It is postulated that the high endemism is the result of introduction of a few ancestral species from South America, followed by rapid speciation in the new habitat. **Bauhinia fryxellii** sp. nov., endemic to San Luis Potosí, Mexico is described and illustrated and **Bauhinia chapulhuacania** nom. nov. (= *B. dipetala* var. *macrophylla* Wunderlin) is proposed. Keys, descriptions, distributional data, and taxonomic index are provided.

The caesalpinioid tribe Cercideae is divided into two subtribes, the Cercidinae and Bauhiniinae (Wunderlin et al., 1981). The Cercidinae consist of three small distinctive genera; *Cercis* with six species in the temperate northern hemisphere, *Griffonia* with four species in Africa, and *Adenolobus* with two species in Africa. The Bauhiniinae contain the large, diverse, pantropical genus *Bauhinia* and the monotypic Madagascan genus *Brenierea*. The approximately 300 species of *Bauhinia* are important components of the floras of low and middle elevations throughout the tropics. The species are about evenly divided between the two hemispheres; however, they are most abundant in northern South America and southern Asia. In the Neotropics they range from southern Texas in the United States southward to northern Argentina. A few species extend into the Antilles and near offshore islands.

Bauhinia has two main phyletic lines, one giving rise to the Bauhinia, Piliostigma, and Barklya groups and the other to the Phanera group (Wunderlin et al., 1981).[3] I confine further remarks here primarily to the Bauhinia group of the genus to which the native, arborescent Middle American species belong. The pantropical Bauhinia group consists of approximately 150 species that are characteristically trees or shrubs (rarely subscandent), often with intrastipular spines, and the calyx spathaceous or dividing to the lip of the hypanthium into 2–5 lobes. Of this group, 27 species are native to Middle America, which is here defined as encompassing Mexico, Central America (including Panama), the Greater Antilles, and the northern Lesser Antilles (Leeward and Windward Islands). Trinidad and Tobago and the southern Lesser Antilles are excluded, since the few *Bauhinia* species occurring there are only northward extensions of those found in South America, which will be treated in subsequent papers.

In Middle America the Bauhinia group occurs in a variety of habitats ranging from tropical rainforest to deciduous forest to desert scrub. Most are shrubs or small trees but a few of the rainforest species are moderate to large trees (e.g. *B. picta* ranges up to 40 meters in height).

Pollination in the Bauhinia group in Middle America is usually by chiropterophily, psychophily, and phanaenophily, with melittophily and ornithophily suspected in some species but unconfirmed. Some species are self-compatible

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[3] A reorganization of the Cercideae, an amplification of the overview by Wunderlin et al. (1981), is underway (Wunderlin et al., in prep.) in which infrageneric taxa will be defined and formally proposed and the phylogeny discussed in detail. For that reason, I have elected not to use categories which might be misconstrued as formal proposals of infrageneric names in this work. The terms "group," "alliance," and "suballiance" as used here are more or less equivalent to subgenus, section, and subsection respectively.

while others are self-incompatible (Heithaus et al., 1974; Heithaus, 1979). Plants with functionally staminate and/or pistillate flowers, usually along with normal hermaphroditic flowers, are found in many of the species.

The seeds of members of the Bauhinia group in Middle America are autochorous in that the fruit valves are explosively dehiscent. Mammaliochory may also be involved in further seed dispersal, e.g. removal by nut- and seed-storing rodents. Ornithochory, although not confirmed for this group, may have played a role in dispersal, especially over water.

Seed beetles (Bruchidae: Bruchinae) have exploited *Bauhinia* seeds as a larval food, *Gibbobruchus* feeding almost exclusively on members of the Bauhinia group (Whitehead & Kingsolver, 1975). Most *Gibbobruchus* species feed on several *Bauhinia* species; none are host specific. *Caryedes* feeds mainly on papilionoid legumes but the *stenocephalus* group feeds on two widespread species of the Phanera group of *Bauhinia* (Kingsolver & Whitehead, 1974).

TAXONOMY

The last comprehensive revision of *Bauhinia* was that of Dietrich (1840), who recognized 81 species. Three to four times that number of additional species have been described since that time. There has been no comprehensive treatment either of a major infrageneric group on a world-wide basis or in a major geographic area (i.e. Neotropics, Paleotropics, or continent) although floras of numerous countries or small geographic regions have included treatments of *Bauhinia* and sometimes segregate genera. Few of these regional treatments agree taxonomically, thus complicating the situation. Specimens collected recently have yielded data that make many of these regional treatments out of date. For example, Schery in 1951 recognized 13 species of *Bauhinia* native to Panama but Wunderlin in 1976 reduced five of them to synonymy and added three others. Of the 13 names used by Schery, only four are retained by Wunderlin. Thus in a span of only 25 years the taxonomy of the genus for Panama has been greatly modified. It is readily apparent that this large and important genus is long overdue for revision. This paper is the first of a series involving a comprehensive revision of the Neotropical species.

Among the floristic treatments of the Neotropical Cercideae during this century, that of Britton and Rose (1930) is of special interest. Britton and Rose, in revising the species of North America (including Mexico, Central America, Panama, and the Antilles), departed from the then current systematic trend by recognizing *Alvesia, Caspareopsis, Casparia,* and *Schnella* as genera distinct from *Bauhinia.* Unfortunately, they erroneously adopted Kunth's concept of *Casparia,* placed in it the type species of *Bauhinia* and redefined *Bauhinia* in the sense of *Pauletia* Cav. In their revision they recognized one species of *Alvesia,* ten of *Bauhinia,* one of *Caspareopsis,* thirty-four of *Casparia,* and nine of *Schnella.* The taxa treated in the revision presented here include those placed in *Bauhinia* and *Casparia* by Britton and Rose. *Alvesia* and *Caspareopsis* constitute introduced Asiatic species and are excluded for that reason. Those placed in *Schnella* by Britton and Rose are members of the Phanera group and will be treated in subsequent works. Three later treatments of *Bauhinia* in countries within the scope of Britton and Rose's work are those of Standley and Steyermark (1946), who treated the species of Guatemala and recognized 13 native species; Schery (1951), who treated the Panamanian members of the genus, also recognizing 13 native species; and Wunderlin (1976) who also treated the Panamanian species, recognizing 11 native species.

A considerable amount of taxonomic confusion at the specific and infraspecific levels plagues *Bauhinia.* This confusion can be in part attributed to the phenotypic plasticity of those vegetative characters that have erroneously been emphasized by various workers. Taxonomists lacking a broad understanding of the genus have placed undue emphasis on vesture, shape, and degree of lobing of leaves. As a result, several wide-ranging, phenotypically polymorphic species have been described a number of times from specimens collected in widely separated localities. On the other hand, some species that had been considered to be polymorphic by some workers are actually composed of two or more distinct taxa. The size of the genus and its great morphological diversity have therefore contributed to a variety of delimitations at all taxonomic levels. As previously stated, all recent work has been done on a regional basis in conjunction with floristic projects and few wide ranging species or species groups have been examined throughout their range by these workers. This has also contributed to the proliferation of superfluous names.

PHYTOGEOGRAPHY AND PHYLOGENY

The 27 species of the Bauhinia group native to Middle America can be divided into three

species alliances herein referred to as the Divaricata, Petiolata, and Aculeata alliances (Table 1). The Divaricata alliance consists of 17 species, all endemic to Middle America except one recently discovered, undescribed species endemic to eastern Brazil. The Petiolata alliance consists of about 14 species in the Neotropics, four of which are endemic to Middle America and three shared with South America. The Aculeata alliance consists of about 80 species in the Neotropics and two in the Paleotropics. Of these, only four occur in Middle America and all are shared with South America. Each of these alliances is further subdivided into suballiances of which by far the largest in Middle America, with 15 species, is the Divaricata suballiance of the Divaricata alliance (Table 1).

The greatest species diversity within the Bauhinia group in Middle America is in Mexico, where 22 of the 27 species treated in this work occur, 11 of which (*B. andrieuxii, B. chapulhuacania, B. coulteri, B. deserti, B. fryxellii, B. jucunda, B. macranthera, B. pes-caprae, B. pringlei, B. ramosissima,* and *B. subrotundifolia*) are endemic. No species of *Bauhinia* is endemic to any other country in Middle America. Of the 11 nonendemic species found in Mexico, eight (*B. cookii, B. dipetala, B. divaricata, B. erythrocalyx, B. jenningsii, B. pansamalana, B. rubeleruziana,* and *B. seleriana*) extend into Central America, some as far south as Costa Rica, two (*B. divaricata* and *B. jenningsii*) range east into the Greater Antilles, one (*B. divaricata*) barely reaches the Lesser Antilles, one (*B. lunarioides*) extends north into southern Texas, and two (*B. pauletia* and *B. ungulata*) are wide ranging species that extend into northern South America. The remaining five species in Middle America are northward extensions of South American species. One of these (*B. beguinotii*) extends north to Panama and Costa Rica, two (*B. picta* and *B. petiolata*) extend north only to Panama, and one (*B. aculeata*) extends north to Panama and is apparently disjunct in El Salvador. The remaining species (*B. multinervia*) occurs in northeastern South America and extends north only into the Lesser Antilles.

The primitive androecium of *Bauhinia* has all ten stamens fertile. The 15 Middle American endemics in the Divaricata suballiance are notable in having a single fertile anther. This character is otherwise found only in the Asian *B. monandra* Kurz and the Madagascan *B. porosa* Boiv. The occurrence of this unusual androecial condition in the Asian and Madagascan species I consider an example of convergent evolution; I do not wish to suggest that they are closely related to the Neotropical monandrous species. Five of the Neotropical monandrous species (*B. chapulhuacania, B. deserti, B. dipetala, B. fryxellii,* and *B. jucunda*) are further distinguished by having the corolla reduced from the five petals typical in the genus to four or less. This character is unique for *Bauhinia* as a whole. *Bauhinia coulteri,* the single member of the Coulteri suballiance of the Divaricata alliance, has flowers with three fertile anthers. This character is shared with only two other Neotropical species, *B. pansamalana,* a member of the Petiolata alliance; and an undescribed species native to eastern Brazil that is a member of the Divaricata alliance. The functionally triandrous condition reappears in a few Paleotropical species of the Bauhinia group and is common in the very distantly related Paleotropical members of the Phanera group of *Bauhinia,* again a case of convergent evolution.

I postulate that propagules of a few progenitor species of the Bauhinia group were disseminated into Central America and Mexico from South America, became isolated, and gave rise to the 20 species endemic in Middle America (see Table 1). I further postulate that the remaining seven species of the Bauhinia group found in Middle America today have more recently migrated into that area from South America.

A hypothetical explanation for the distribution of the Middle American species of the Bauhinia group can be based on current theories of continental drift. Assuming that the ancestral Caesalpinioideae evolved in the Late Cretaceous (before 65 m.y. BP), it reasonably follows *Bauhinia* evolved, began to diversify, and spread from its probable center of origin in Africa to South America and Eurasia in the Paleogene. The further back in the Paleogene time that *Bauhinia* and the various constituent lines within the genus evolved, the shorter the water gaps that it would have to traverse between Africa and South America, the probable pathway between the Old and New World. Once the progenitor species of *Bauhinia* reached South America, it probably rapidly speciated there in relative isolation from Africa and North America. Until the early Late Eocene (ca. 50 m.y. BP) South America was probably closer to Africa than to North America (Raven & Axelrod, 1974) which would have made movement of the genus into North America more difficult than from Africa to South America. However, *Bauhinia* seems to have been in North

TABLE 1. Arrangement of the alliances and suballiances of *Bauhinia* within the arborescent Bauhinia group represented in the Neotropics with emphasis on those occurring in Middle America. Species endemic to Middle America are indicated by an asterisk (*). Formal proposal of infrageneric taxa will be made and reasons discussed in detail in the proposed reorganization of the Cercideae (Wunderlin et al., in prep.).

Divaricata Alliance—Unarmed; calyx spathaceous; fertile stamens 1 or 3; pollen 3-colpor(oid)ate, sexine reticulate or striato-recticulate, occasionally with elongate supratectal processes.
- Divaricata Suballiance—Petals long-clawed; fertile stamen 1.
  - *B. chapulhuacania* Wunderlin*
  - *B. deserti* (Britt. & Rose) Lundell*
  - *B. dipetala* Hemsl.*
  - *B. divaricata* L.*
  - *B. erythrocalyx* Wunderlin*
  - *B. fryxellii* Wunderlin*
  - *B. jenningsii* P. Wils.*
  - *B. jucunda* Brandeg.*
  - *B. lunarioides* A. Gray ex S. Wats.*
  - *B. macranthera* Benth. ex Hemsl.*
  - *B. pes-caprae* Cav.*
  - *B. pringlei* S. Wats.*
  - *B. ramosissima* Benth. ex Hemsl.*
  - *B. rubeleruziana* Donn. Sm.*
  - *B. subrotundifolia* Cav.*
- Coulteri Suballiance—Petals sessile; fertile stamens 3, adjacent.
  - *B. coulteri* Macbr.*

Petiolata Alliance—Unarmed; calyx spathaceous; fertile stamens 3 or 10 (also 5 in extra-Middle American species); pollen inaperturate, sexine reticulate with blunt, spinelike infratectal processes.
- Petiolata Suballiance—Fertile stamens 10.
  - *B. andrieuxii* Hemsl.*
  - *B. beguinotii* Cuf.
  - *B. cookii* Rose*
  - *B. petiolata* (Mutis ex DC.) Triana ex Hook. f.
  - *B. picta* (H.B.K.) DC.
  - *B. seleriana* Harms*
  - (7 additional species in South America.)
- Pansamalana Suballiance—Fertile stamens 3, separated from each other by a staminode.
  - *B. pansamalana* Donn. Sm.*

Aculeata Alliance—Armed with intrastipular spines or unarmed; calyx spathaceous or splitting to lip of hypanthium; fertile stamens 5 or 10; pollen inaperturate, 3–6-colpate, or 3–4-colporoidate, sexine reticulate with clavate supratectal processes or 3–6-poroidate, sexine with blunt, spinelike infratectal processes.
- Aculeata Suballiance—Fertile stamens 5 or 10; pollen inaperturate, 3–6-colpate, or 3–4-colporoidate, sexine reticulate with clavate supratectal processes.
  - *B. aculeata* L.
  - *B. pauletia* Pers.
  - *B. ungulata* L.
  - (Ca. 70 additional species in South America and 2 in Paleotropics.)
- Multinervia Suballiance—Fertile stamens 10; pollen 3–6-poroidate, sexine reticulate with blunt, spinelike infratectal processes.
  - *B. multinervia* (H.B.K.) DC.
  - (5 additional species in northern South America.)

America long enough to allow the differentiation of the endemic species. This pattern is similar to that found in the Cactaceae, Krameriaceae, Liliaceae-Allieae, Loasaceae, Martyniaceae, Nyctaginaceae, Onagraceae-*Fuchsia*, Tecophilaeaceae, and Zygophyllaceae (Raven & Axelrod, 1974; Berry, 1982; Peter Raven, pers. comm.).

I suggest that propagules of one or more members of the Divaricata alliance were disseminated to North America and subsequently diversified. Members of this alliance possess the most advanced characters (e.g. reduction in fertile anther and petal number) and are now restricted to North America and the Antilles and a single species disjunct to eastern Brazil.

Propagules of the Petiolata alliance were also disseminated to Central America and gave rise to the endemic *B. pansamalana*, the only known member of the Pansamalana suballiance, which is characterized by three fertile stamens, a feature shared in the Neotropical species only by *B. coulteri* and a recently discovered, undescribed species in eastern Brazil, both of the Divaricata alliance. Similarly, other propagules of the Petiolata alliance could have given rise to the three other endemic species of the Petiolata alliance, *B. andrieuxii* Hemsl., *B. cookii*, and *B. seleriana* Harms.

It is probable that the wide distribution in Middle America today of species such as *B. pauletia* and *B. ungulata*, the presence of *B. aculeata* in Panama and disjunct to El Salvador, of *B. beguinotii* in Panama and Costa Rica, and of *B. picta* and *B. petiolata* in Panama are the result of more recent migration from centers in northern South America.

The presence in the Greater Antilles of only *B. divaricata*, a widespread weedy species of

Mexico south to Nicaragua, and *B. jenningsii,* also found in the Yucatán Peninsula of Mexico, Guatemala, and Belize, indicates *Bauhinia* is probably a relatively recent member of the flora of the Greater Antilles.

The occurrence of two northern South American species, *B. aculeata* and *B. multinervia,* in the Windward and Leeward Islands suggests that these species may also be recent migrants into that area.

Furthermore, five species of *Bauhinia* that belong to the Phanera group, not treated in this revision, also occur in Middle America. Four of these (*B. glabra* Jacq., *B. guianensis* Aubl., *B. hymenaeifolia* Triana ex Hemsl., and *B. microstachya* (Raddi) Macbride) are wide-ranging South American species, and one (*B. reflexa* Schery) is endemic to Panama but closely related to South American species. These also appear to represent relatively recent additions to the flora of Middle America.

Finally, about 20 species, of which seven have become naturalized, are cultivated in Middle America. These also are not treated in this revision but will be dealt with in subsequent floristic works. They include four species native to Asia (*B. acuminata* L., *B. monandra* Kurz, *B. purpurea* L., and *B. variegata* L.), two to Africa (*B. galpinii* N. E. Br. and *B. tomentosa* L.), and one to South America (*B. bauhinioides* (Mart.) Macbr.).

Systematic Treatment

BAUHINIA L., Sp. Pl. 374. 1753; non Kunth, 1824; nec Raf., 1838. LECTOTYPE: *Bauhinia divaricata* L.

Pauletia Cav., Icon. 5: 5. 1799. LECTOTYPE: *Pauletia inermis* Cav. [= *Bauhinia ungulata* L.].

Amaria Mutis, Sem. Nuev. Rey. Gran. 2: 25. 1810. LECTOTYPE: *Amaria petiolata* Mutis ex DC. [= *Bauhinia petiolata* (Mutis ex DC.) Triana ex Hook. f.].

Bauhinia Kunth, Ann. Sci. Nat. (Paris) 1: 85. 1824; non L., 1753; nec Raf., 1838. LECTOTYPE: *Bauhinia aculeata* L.

Casparia Kunth, Ann. Sci. Nat. (Paris) 1: 85. 1824. TYPE: *Casparia pes-caprae* (Cav.) H.B.K. [= *Bauhinia pes-caprae* Cav.].

Perlebia Mart. in Spix & Mart., Reise Bras. 2: 555. 1828; non DC., 1829 [Apiaceae]; nec Schmitz, 1973. TYPE: *Perlebia bauhinioides* Mart. [= *Bauhinia bauhinioides* (Mart.) Macbr.].

Bauhinia Raf., Sylva Tellur. 121. 1838; non L., 1753; nec Kunth, 1824. LECTOTYPE: *Bauhinia aculeata* L.

Cansenia Raf., Sylva Tellur. 122. 1838. LECTOTYPE: *Cansenia ungulata* (L.) Raf. [= *Bauhinia ungulata* L.].

Mandarus Raf., Sylva Tellur. 122. 1838. LECTOTYPE: *Mandarus divaricatus* (L.) Raf. [= *Bauhinia divaricata* L.].

Ariaria C. Marq., Estud. Arq. Etno. Amer. 1: 141. 1920. TYPE: *Ariaria superba* C. Marq. [= *Bauhinia tarapotenis* Benth.].

Perlebia Schmitz, Bull. Jard. Bot. Nat. Belg. 43: 381. 1973, nom. inval.; non Mart., 1828; nec DC., 1829 [Apiaceae]. Type of *Perlebia* Mart. excluded and type of *Perlebia* Schmitz not designated.

Other generic synonyms exist for *Bauhinia,* but only those that apply to the Neotropical species of the Bauhinia group are listed here. Typification of generic names listed above is given in Wunderlin (1976a).

Trees or shrubs, with intrastipular spines or unarmed; stems and branches terete or nearly so. Leaves entire, bilobate or bifoliolate; stipules small, linear to lanceolate to ovate, caducous or rarely persistent; intrastipular excrescences minute or sometimes adpetiolar enlarged and subulate or forming an intrastipular spine. Inflorescences racemose, paniculate, or flowers paired or solitary, terminal, or subterminal and axillary; bract solitary, small, linear to ovate; bracteoles 2, similar to bracts but smaller; flower buds linear to lanceolate; sepals 5, valvate, united nearly to apex, usually with free tips, limb spathaceous or splitting into 2–5 lobes to or nearly to hypanthium lip; nectaries usually present on interior of calyx at base; hypanthium cyathiform to tubular; petals 5, rarely fewer, free, imbricate, usually subequal, or less commonly unequal, clawed or sessile, spatulate to filiform, white, pink to red, green, or yellow, uppermost usually darker or differing in pattern; stamens 10, basally connate, diplostemonous, the alternate shorter, 1, 3, 5, or all 10 fertile, sterile stamens (if present) variously reduced, filaments of fertile stamens filiform or stout, anthers ovate to linear, apex emarginate to apiculate, base sagittate, dorsifixed, versatile, theca opening longitudinally; pollen spheroid to peroblate, inaperturate, 3–6-colpate, or 3–4-colpor(oid)ate, 3–6-poroidate, sexine striate, striato-reticulate, or reticulate, sometimes with supratectal or infratectal processes; gynoecium often equalling androecium, gynophore long, acentric, adnate to abaxial wall of hypanthium or free, ovary several-ovulate, style filiform or stout, stigma capitate or oblique. Fruit woody, elastically dehiscent or indehiscent legume; seeds laterally compressed, surface ob-

scurely marked, albumen present, radicle straight or nearly so, cotyledons flat, funicular aril-lobes short, each appressed to seed at maturity and forming a narrow scar.

Because of the great morphological diversity of the genus worldwide, the above description is applicable only to the Neotropical species of the *Bauhinia* group.

KEY TO SPECIES

1a. Plants armed with evident intrastipular spines.
 2a. Petals white, elliptic to obovate; fertile stamens 10; buds linear-lanceolate, 3–4(–5.5) cm long .... 1. *B. aculeata*
 2b. Petals green, filiform; fertile stamens 5; buds filiform, 8–10(–12) cm long .... 18. *B. pauletia*
1b. Plants unarmed (if apetiolar intrastipular excrescence enlarged, then merely subulate and 2 mm long or less).
 3a. Fertile stamen 1.
  4a. Corolla of usually 1–3, rarely 4, usually unequal petals, sometimes with 1 or more vestigial.
   5a. Leaves with lobes less than 3 cm wide and conspicuously divaricate.
    6a. Corolla usually with only 1 petal well-developed, others vestigial or absent; style less than 1 cm long at anthesis, stout; endemic to southeastern San Luis Potosí, Mexico .... 11. *B. fryxellii*
    6b. Corolla usually with 3–4 petals well-developed, others vestigial or absent; style over 1 cm long at anthesis, filiform; endemic to central Veracruz, Mexico .... 13. *B. jucunda*
   5b. Leaves with lobes over 3 cm wide and parallel or only slightly divaricate.
    7a. Leaves (6–)10–15(–30) cm long; legume (15–)18–25(–30) cm long .... 4. *B. chapulhuacania*
    7b. Leaves (3–)5–11(–12) cm long; legume (8–)10–15(–18) cm long.
     8a. Leaves chartaceous, usually lobed less than half their length (rarely lobed to one-half), sinus between lobes usually acute at base .... 8. *B. dipetala*
     8b. Leaves subcoriaceous, usually lobed half or more their length (rarely lobed less than half), sinus between lobes usually obtuse to rounded at base .... 7. *B. deserti*
  4b. Corolla always of 5, subequal petals.
   9a. Petals distinctly pink, purple, or red.
    10a. Leaves bifoliolate, 1–2 cm long, leaflets 2–(3)-nerved .... 23. *B. ramosissima*
    10b. Leaves bilobate or entire (rarely bifoliolate in some forms of *B. macranthera*), 4 cm long or longer, 7–9-nerved.
     11a. Inflorescence less than 10-flowered; petals pink, blade subequalling the pilose claw; lower surface of young leaves glabrous or pubescent, but not with yellowish-brown hairs .... 15. *B. macranthera*
     11b. Inflorescence 20-flowered or more; petals brick red, blade about twice as long as glabrate claw; lower surface of young leaves with yellowish-brown hairs .... 24. *B. rubeleruziana*
   9b. Petals white or cream (sometimes turning pinkish in age in *B. divaricata*, but then branches and undersurface of young leaves never with yellowish-brown hairs), or white with a conspicuous red median stripe.
    12a. Leaves bifoliolate .... 14. *B. lunarioides*
    12b. Leaves bilobate or entire.
     13a. Leaves entire .... 12. *B. jenningsii*
     13b. Leaves bilobate.
      14a. Petals white with conspicuous red median stripe .... 22. *B. pringlei*
      14b. Petals white (sometimes turning pinkish in age in *B. divaricata*), without a conspicuous red median stripe.
       15a. Petals pilose.
        16a. Leaves suborbicular, bilobate for about half their length; flowers buds always erect .... 26. *B. subrotundifolia*
        16b. Leaves ovate to oblong, bilobate for ¾ or more their length; flowers buds reflexed when young, erect at anthesis .... 19. *B. pes-caprae*
       15b. Petals glabrous or glabrate.
        17a. Calyx bright red, free tips obsolete .... 10. *B. erythrocalyx*
        17b. Calyx greenish or rarely with dull red tinge, free tips ca. 2 mm long .... 9. *B. divaricata*
 3b. Fertile stamens 3 or 10.
  18a. Fertile stamens 3.
   19a. Petals pink (rarely white) sessile; leaves suborbicular (2–)3–5(–6) cm long .... 6. *B. coulteri*
   19b. Petals white, short-clawed; leaves ovate, 12–22 cm long .... 17. *B. pansamalana*

18b. Fertile stamens 10.
  20a. Leaves entire (sometimes bilobate on same plant).
    21a. Shorter stamens connate for about half their length; leaves with inner pair of nerves usually closer to midrib than to outer adjacent nerves .... 3. *B. beguinotii*
    21b. Shorter stamens free nearly to base; leaves with inner pair of nerves usually equidistant or closer to outer adjacent nerves than to midrib .... 20. *B. petiolata*
  20b. Leaves always bilobate.
    22a. Inflorescence, lower surface of leaves, and fruits brown tomentose ... 25. *B. seleriana*
    22b. Inflorescence, lower surface of leaves, and fruits other than brown tomentose.
      23a. Leaves less than 2.5 cm long, apex of lobes rounded .... 2. *B. andrieuxii*
      23b. Leaves 5 cm long or longer, apex of lobes obtuse to caudate.
        24a. Petals light sulfur-yellow; fruits 5–7 cm long .... 5. *B. cookii*
        24b. Petals white or pinkish with roseate center; fruits over 10 cm long.
          25a. Calyx splitting to hypanthium into 2–5 lobes; petals with blades linear to filiform.
            26a. Flower buds 4–5 cm long; fruits ca. 1 cm wide .... 27. *B. ungulata*
            26b. Flower buds 7–10 cm long; fruits ca. 2 cm wide .... 16. *B. multinervia*
          25b. Calyx spathaceous; petals with blades ovate-elliptic.
            27a. Staminal sheath distinctly ligulate .... 21. *B. picta*
            27b. Staminal sheath not ligulate .... 3. *B. beguinotii*

1. **Bauhinia aculeata** L., Sp. Pl. 374. 1753; non Vell., 1825. TYPE: Colombia or Venezuela: *Herb. Clifford* (holotype, BM; photograph of holotype, IJ).

Bauhinia emarginata Mill., Gard. Dict. ed. 8. 1768; non Jack, 1822; nec Wall., 1831; nec Roxb. ex G. Don, 1832. TYPE: Colombia. Bolívar: Cartagena, *Houstoun s.n.* (holotype, BM; photograph of holotype, IJ, US).

Bauhinia rotundata Mill., Gard. Dict. ed. 8. 1768. TYPE: Colombia. Bolívar: Cartagena, *Houstoun s.n.* (holotype, BM; photograph of holotype, US).

Bauhinia ungula Jacq., Frag. Bot. 22. 1801; non Willd. ex Steud., 1840. TYPE: Venezuela: *Jacquin s.n.* (holotype, W, not seen).

Pauletia glandulosa H.B.K., Nov. Gen. Sp. Pl. 6: 314. 1824. *Bauhinia glandulosa* (H.B.K.) DC., Prodr. 2: 513. 1825. TYPE: Venezuela. Sucre: Cumaná, *Humboldt 47* (holotype, P, not seen; microfiche, MO; isotype, B(W), not seen; photograph of isotype, F, MO, NY, US).

Bauhinia bredemeyeri Vog., Linnaea 13: 302. 1839. TYPE: Venezuela. Federal District: Near Caracas, *Bredemeyer s.n.* (holotype, B, not seen; fragment of holotype, F; photograph of holotype, F, MO, NY, US).

Bauhinia ungula Willd. ex Steud., Nom. Bot. ed. 2. 1: 191. 1840, pro syn.; non. Jacq., 1801.

Bauhinia mollicella Blake, Contr. Gray Herb. 53: 32. 1918. TYPE: Venezuela. Vicinity of Las Cumbres, *Curran & Hammon 1024* (holotype, GH, not seen; isotypes, NY, US).

Bauhinia miranda Pittier, Trab. Mus. Com. Venez. 1: 13. 1927. TYPE: Venezuela. Miranda: Los Mariches, on new road to Santa Lucía, *Pittier 11783* (holotype, VEN, not seen; isotypes, NY, P, US; photograph of NY isotype, NY).

Bauhinia mollifolia Pittier, Trab. Mus. Com. Venez. 1: 14. 1927. TYPE: Venezuela. Cojedes: Between San Rafael de Onoto and Agua Blanca, *Pittier 11726* (holotype, VEN, not seen; isotypes, NY, US).

Bauhinia schultzei Harms, Repert. Spec. Nov. Regni Veg. 24: 210. 1928. TYPE: Colombia. Magdalena: Sierra Nevada de Santa Marta, upper Río Frío, *Schultze 428* (holotype, B, not seen; fragment of holotype, F; photograph of holotype, F, MO, NY, US).

Bauhinia albiflora Britt. & Rose, N. Amer. Fl. 23: 203. 1930. TYPE: El Salvador. Sonsonate: Vicinity of Sonsonate, *Standley 22373* (holotype, US; isotype, NY).

Shrubs or small trees up to 8(–10) m tall; branches tomentose when young, soon glabrate, armed with 1–2 intrastipular spines up to 1 cm long. Leaves chartaceous, suborbicular to broadly lanceolate, emarginate or bilobate for ⅓, rarely to ½ their length, lobes parallel or slightly divergent, 3–6 cm long, 2.5–5.0 cm wide, base cordate to rounded, apex of lobes rounded to acute, margins smooth, tomentose, strigose or glabrate on both surfaces, 7–9-nerved; petiole 0.5–3.0 cm long, slightly canaliculate, tomentose, strigose, or glabrate; stipules linear, ca. 4 mm long, caducous; adpetiolar intrastipular excrescence forming a frequently reflexed spine, others minute. Inflorescences short racemose, less commonly geminate or 1-flowered, subterminal, axillary, racemes 3–10-flowered, rachis tomentose, strigose, or glabrate, buds linear-lanceolate 3–4 cm long, tomentose, strigose, or glabrate, free tips up to 1.5 mm long; bract linear, 2–5 mm long; bracteoles similar to bract; pedicels 0.5–1.0 cm long, tomentose or strigose; hypanthium tubular, 0.3–1.0 cm long; calyx spathaceous at anthesis; petals 5, subequal, white, 3–8(–10) cm long, blade

narrowly elliptic to obovate, 2–10 times as long as claw, (0.5–)1.0–2.5 cm wide, glabrous, claw sparsely pilose to glabrous; fertile stamens 10, ca. ⅘ the length of petals, 5 alternate ones shorter, filaments slender, arcuate, sparsely pilose at base, short-connate at base for 1–5 mm, anthers linear, 4–7 mm long; pollen spheroid, inaperturate, sexine reticulate with clavate supratectal processes; gynoecium nearly equalling stamens, arcuate, ovary and gynophore densely pilose, style glabrate, gynophore nearly equalling to ½ as long as style, stigma capitate. Fruit linear to narrowly elliptic, apiculate with persistent style, 7–15 cm long, 1.5–2.5 cm wide, light brown, pubescent at maturity, sometimes becoming glabrate in age, gynophore 1–2 cm long, puberulent; seeds oblong to suborbicular, 6–11 mm long, 5–8 mm wide surface dull, dark brown, funicular aril-lobe scars equal, 2.0–2.5 mm long.

Bauhinia aculeata consists of two subspecies, the typical form, to which the Middle American material is referred, and subsp. *grandiflora* (Juss.) Wunderlin, which occurs in Bolivia, Ecuador, and Peru. The latter is distinguished by larger leaves, fruits, and by flowers with a conspicuously elongated hypanthium. In Middle America *B. aculeata* is native to El Salvador and Panama in Central America and Barbados and Grenada in the Lesser Antilles. It is also known from Antigua as an escape from cultivation. Outside Middle America, this species is native to Colombia and Venezuela where it is especially common. The species is found at elevations ranging from near sea level up to 1,700 m in open tropical deciduous forest or in disturbed sites. It flowers throughout the year but most abundantly from March to June. It is sometimes cultivated within and outside its natural range as an ornamental.

The taxonomy of the *B. aculeata* complex is still only partly understood; there are a number of names applied to entities in South America that may or may not be distinct. *Bauhinia aculeata* is closely related to about 30 additional South American and two Old World species. Britton and Rose described *Bauhinia albiflora* as having five fertile stamens, but an examination of the type material revealed it to have ten.

Bauhinia aculeata is highly polymorphic as is evidenced by the extensive synonymy. However, it is easily distinguished from all other Middle American species because it is the only spiny species with large, white, showy flowers and ten fertile stamens. The only other spiny species in Middle America, *B. pauletia,* has inconspicuous green flowers with filiform petals and only five fertile stamens.

Bauhinia aculeata is believed to be bat-pollinated and possibly also moth-pollinated, as appear to be many of its allies in South America.

In Venezuela this species is known as "Pata de Vaca," "Dibrito," "Quimbrapoto," "Guarapa," or "Urapa."

Representative specimens: EL SALVADOR. SAN MIGUEL: Vicinity of San Antonio N of Ciudad Barrios, *Allen & Armour 6867* (F). SONSONATE: Vicinity of Acajutla, *Standley 21983* (NY, US). PANAMA. COCLÉ: La Pintada, *León 12* (MO). PANAMÁ: E of Pacora, *Woodson et al. 735* (MO, NY, US). ANTIGUA. Upper Cedar Hill, *Box 1193* (F, UC, US). BARBADOS. St. Thomas, Hopewell Gully, *Bovell 208* (UCWI). GRENADA. St. George's, *Broadway s.n.* (F, NY, US).

2. **Bauhinia andreiuxii** Hemsl., Diag. Pl. Nov. 48. 1880. TYPE: Mexico. Oaxaca: Near Oaxaca, *Andrieux 411* (holotype, K; isotypes, G, not seen, P; fragment of G isotype, F; photograph of G isotype, F, MO, US).

Shrubs or small trees; branches tuberculate, tomentose when young, soon glabrate. Leaves chartaceous, suborbicular or broader than long, bilobate up to ½ their length, lobes slightly divergent, 1.0–2.2 cm long, 1.5–3.0 cm wide, base cordate to rounded, apex of lobes rounded, upper surface glabrous, lower surface tomentellous, 7–9-nerved; petiole 5–15 mm long, slightly canaliculate, tomentellous; stipules ovate, ca. 1 mm long, caducous; adpetiolar intrastipular excrescence fused and forming a subulate projection ca. 1 mm long, others minute. Inflorescences racemose, congested, terminal, 3–8-flowered, rachis strigose or tomentellous, buds linear-lanceolate, 12–18 mm long, strigose or tomentellous, free tips ca. 1.5 mm long; bract lanceolate, ca. 1.5 mm long; bracteoles similar but slightly smaller than bract; pedicels ca. 5 mm long, strigose or tomentellous; hypanthium cyathiform, 2–3 mm long; calyx spathaceous at anthesis; petals 5, subequal, white, broadly elliptic, ca. 1 cm long, blade 4–6 mm wide, glabrous, claw ca. 1 mm long, glabrous; fertile stamens 10, 5 nearly equalling petals, alternate 5 ca. ½ the length of petals, unequally short-connate at base for 1–3 mm, filaments slender, glabrous, anthers linear oblong, ca. 2 mm long on longer stamens, ca. 1.5 mm long on shorter stamens; pollen spheroid, inaperturate, sexine reticulate with blunt, spinelike, in-

fratectal processes; gynoecium nearly equalling petals, tomentose, gynophore nearly equalling style in length, stigma capitate. Fruit linear, apiculate with persistent style, 8–10 cm long, ca. 1.5 cm wide, dark brown, tomentose; seeds not seen.

Bauhinia andrieuxii is a wide-ranging but infrequently collected species occurring in western Mexico from Sinaloa to Oaxaca. It occurs in deciduous thorn scrub at elevations from near sea level up to around 1,800 m.

This species is distinguished from other species of *Bauhinia* with ten fertile stamens in the area by its small leaves, which are suborbicular or broader than long. It is most closely related to *B. seleriana.*

The pollinators of this species are probably butterflies or possibly bees.

Specimens examined: MEXICO. MORELOS: Cañón de Lobos, Km 14 on Cuernavaca-Yautepec road, *Fryxell 764* (MEXU); Cañón de Lobos, *Vázquez 1776* (MEXU). OAXACA: Monte Albán, *Rose & Hough 4590* (NY, US); *Sousa et al. 6077* (MEXU, MO); Mitla, *Smith 107* (US). SINALOA: Cerro Llano Redondo, W of Caimanero, *Gentry 7018* (NY). Without precise locality: *Andrieux 371* (P).

3. **Bauhinia beguinotii** Cuf., Arch. Bot. Sist. 9: 192. 1933. TYPE: Costa Rica. Limón: Between Waldeck and Río Barbilla, *Cufondontis 664* (holotype, W, not seen; photograph of holotype, F, MO, US).

Shrubs or small trees up to 6 m tall; branches brown tomentose to tomentellous when young, soon glabrate. Leaves chartaceous, oblong-ovate, entire to shallowly bilobate, 10–24 cm long, 5–16 cm wide, base rounded to truncate, apex of entire leaf or lobes acuminate to caudate, upper surface glabrous, lower surface brown tomentellous to glabrate, 7–9-nerved; petioles 1.5–3.5 cm long, slightly canaliculate, glabrate; stipules broadly ovate, apiculate, 1.0–1.5 mm long, persistent; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 1 mm long, others minute. Inflorescences racemose, terminal, or subterminal and axillary, racemes 5–10-flowered, rachis brown tomentose to tomentellous, buds elliptic-lanceolate, 1.5–2.0 cm long, brown tomentose, free tips minute; bract ovate, ca. 1 mm long; bracteoles similar to bract; pedicels 2–5 mm long, brown tomentose; hypanthium campanulate, 5–6 mm long; calyx spathaceous at anthesis; petals 5, subequal, white, 2.5–3.0 cm long, blade oblanceolate, 8–13 mm wide, glabrous, claw 3–5 mm long, glabrous; fertile stamens 10, the 5 longer ¾ the length to nearly equalling the petals, alternate 5 stamens shorter, short-connate for ca. ½ the length of shorter stamens, filaments sparsely pilose toward base, anthers triangular at anthesis, ca. 3 mm long on longer stamens, ca. 2 mm long on shorter stamens, sparsely pilose to glabrate; pollen spheroid, inaperturate, sexine reticulate with blunt, spinelike processes; gynoecium nearly equalling longer stamens, brown tomentose, gynophore nearly equalling style, stigma capitate. Fruit linear, apiculate with persistent style, 12–15 cm long, 2 cm wide, brown, minutely strigose to glabrate, gynophore 1.0–1.5 cm long, glabrate; seeds not seen.

Bauhinia beguinotii is a rare species known in Middle America only from Costa Rica and Panama, where it occurs in tropical evergreen forest at elevations from near sea level up to about 400 m.

Bauhinia beguinotii is a member of the Petiolata alliance, which is essentially a South American group and includes *B. petiolata* and *B. cookii.* It is less closely related to *B. pansamalana,* also of this alliance, and differs in having ten rather than three fertile stamens. *Bauhinia beguinotii* is distinguished from *B. petiolata,* its most closely related species in Central America, by shorter stamens connate for about half their length rather than being free nearly to the base and by leaves with the inner pair of nerves closer to the midrib than to the outer adjacent nerves rather than equidistant or closer to the outer nerves.

Bauhinia beguinotii is known outside Middle America only from Gorgona Island, Nariño Province, Colombia. The Colombian material is recognized as var. *gorgonae* (Killip ex Cowan) Wunderlin and is distinguished by leaves deeply bilobate or bifoliolate rather than entire or only slightly bilobate. Since the degree of lobing in leaves of *Bauhinia* is often quite variable, further collections may prove var. *gorgonae* not to be distinct from the typical form found in Panama and Costa Rica.

Specimens examined: COSTA RICA. LIMÓN: Drainage of the Río Estrilla Valley, *Shank & Molina 4466* (F, US). PANAMA. PANAMÁ: El Llano-Cart-Tupile road, 16 km N of Pan-American Highway at El Llano, *Nee 9362* (MO); 14.8 km N of the Pan-American Highway, *Folsom & Maas 5202* (MO); ca. 10 km N of Pan-American Highway, *Nee et al. 8881* (MO); 10–12 km N of Pan-American Highway, *Mori & Kallunki 2847* (MO).

4. Bauhinia chapulhuacania Wunderlin, nom. nov. *Bauhinia dipetala* var. *macrophylla* Wunderlin, Southwest. Nat. 13: 104. 1968. TYPE: Mexico. Hidalgo: Near Chapulhuacan, *Moore 2883* (holotype, GH).

Trees up to 6 m tall; branches strigose when young, soon glabrate. Leaves subcoriaceous, broadly ovate, bilobate about ¼–⅓ their length, lobes slightly divergent, (6–)10–15(–30) cm long, (5–)10–15(–25) cm wide, base cordate, apex of lobes rounded to obtuse, margins smooth or nearly so, upper surface glabrous, lower surface minutely brown strigose below when young, glabrate in age, 11-nerved, petiole 2.5–4.0 cm long, slightly canaliculate, brown strigose; stipules ovate-lanceolate, 2.0–2.5 mm long, persistent; adpetiolar intrastipular excrescence enlarged and forming a subulate projection ca. 1.5 mm long, others minute. Inflorescence racemose, terminal, or subterminal and axillary, 20–30-flowered, rachis strigose, buds linear, 2–3 cm long, strigose, free tips up to 2 mm long; bract lanceolate, ca. 1.5 mm long; bracteoles similar to bract but smaller; pedicels 1.0–1.5 cm long, strigose; hypanthium elongate-campanulate, 6–10 mm long; calyx spathaceous at anthesis; petals 2, subequal, linear, tapering to base, 1.0–2.0 cm long, 0.5–1.5 mm wide, brown pilose on inner surface; fertile stamen 1, 2.5–4.0 cm long, filament slender, arcuate, glabrate, short-connate at base with staminodes, anther linear-oblong, green, 8–12 mm long, glabrate; staminodes 9, subequal, 4.5–13.0 mm long, connate for ca. ¾ their length, brown pilose on inner surface, abortive anthers absent; pollen spheroid, 3-colporoidate, sexine striato-reticulate with elongate supratectal processes; gynoecium ca. equalling fertile stamen, arcuate, tomentose, style and gynophore sparsely tomentellous, gynophore ca. equalling style, stigma subclavate, hardly differentiated from style. Fruit linear, apiculate with persistent style, (15–)18–25(–30) cm long, 1.5–2.0 cm wide, dark brown, sparsely brown strigose, gynophore 2.5–4.0 cm long; seeds broadly oblong, 10–12 mm long, 8–10 mm wide, surface dull, dark brown, funicular aril-lobe scars subequal, ca. 3 mm long.

Bauhinia chapulhuacania is a rare species endemic to southeastern San Luis Potosí and northernmost Hidalgo, Mexico where it occurs in open, mixed, mesic forest at 700 to 900 m elevation.

This species is most closely related to *B. dipetala* and *B. deserti*, both of which are characterized by two inconspicuous green petals. *Bauhinia chapulhuacania* occurs over 100 miles to the north of the range of these other two related species and differs in larger leaves and fruits. Because of the close resemblance of its flower to that of *B. dipetala*, *B. chapulhuacania* was originally described as a variety of that species. However, examination of additional collections indicates that it is best treated as a distinct but closely related species and it is here elevated to specific rank. Since the name *B. macrophylla* is preoccupied (*B. macrophylla* Poir., Encyc. Suppl. 1: 600. 1810 [= *B. guianensis* Aubl.]), a new name must be chosen.

Bauhinia chapulhuacania is undoubtedly bat-pollinated as are its close relatives *B. deserti* and *B. dipetala*.

Specimens examined: MEXICO. HIDALGO: S of Tamazunchale, *Barkley & Webster 7264* (F, MEXU, TEX); near Hidalgo-San Luis Potosí border, Km 343–344 on highway below Chapulhuacan, *Moore & Wood 3652* (MEXU, UC, US); 7 mi. S of Chapulhuacan along MEX 85, *Wunderlin 5050* (MO, USF). SAN LUIS POTOSÍ: 31 mi. S of Ciudad Valles along Highway 85, *McGregor et al. 857* (US); Puerto Verde, 64 km W of Ciudad Valles on highway to Río Verde, *Fryxell & Anderson 3605* (MO, USF); near the waterfall at El Salto, *King 3920* (F, NY, TEX, UC, US).

5. Bauhinia cookii Rose in Britt. & Rose, N. Amer. Fl. 23: 205. 1930. TYPE: Costa Rica. Alajuela: Cuesta de la Vieja, road to San Carlos, *Cook & Doyle 41* (holotype, US; fragment of holotype, NY; isotype, US).

Casparia calderonii Rose in Britt. & Rose, N. Amer. Fl. 23: 217. 1930. *Bauhinia calderonii* (Rose) Lundell, Phytologia 1: 214. 1937. *Bauhinia calderonii* (Rose) Standl. & Steyerm., Publ. Field, Mus. Nat. Hist., Bot. Ser. 23: 161. 1944. Superfluous combination for *Bauhinia calderonii* (Rose) Lundell. TYPE: El Salvador. Sonsonate: San Julián, *Calderón 2226* (holotype, US; isotype, US; fragment of isotype, NY).

Bauhinia gigas Lundell, Phytologia 1: 213. 1937. TYPE: Belize. El Cayo: Valentín, *Lundell 6298* (holotype, MICH; isotypes, NY, US).

Trees up to 15(–40) m tall; branches strigose or puberulent when young, soon glabrate. Leaves submembranaceous or chartaceous, broadly ovate, bilobate for ½ or more their length, lobes divaricate, 5–10(–15) cm long, 7–10(–12) cm wide, base cordate to truncate, apex of lobes acute to obtuse, margins smooth, upper surface glabrous, lower surface strigose, at least on nerves, 7–9-nerved; petioles 2–3(–5) cm long, slightly canaliculate, strigose; stipules lanceolate, ca. 1.5 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate pro-

jection up to 1.5 mm long, others minute. Inflorescences paniculate, congested into fasciculate clusters, sometimes produced before the leaves and appearing cauliflorus or ramiflorus, 15–60-flowered, rachis and rachilla strigose, buds linear-elliptic, 8–10 mm long, strigose, free tips minute; bract ovate-lanceolate, ca. 1 mm long; bracteoles similar but slightly smaller than bract; pedicels 5–7 mm long, strigose; hypanthium cyathiform, 2–3 mm long; calyx spathaceous at anthesis; petals 5, subequal, light sulfur-yellow, elliptic to oblanceolate, sessile or short clawed, 10–15 mm long, 5–7 mm wide, glabrate; fertile stamens 10, 5 nearly equalling petals, alternate ones ca. ½ their length, glabrate, short-connate at base for ca. 1 mm, lacinate rim projecting above point of adnation, filaments slender, anthers linear-oblong, those of longer stamens ca. 2 mm long, of shorter stamens ca. 1.5 mm long; pollen spheroid, inaperturate, sexine reticulate with blunt, spinelike infratectal processes; gynoecium ca. ½ the length of petals and ca. equalling shorter stamens, gynophore ca. equalling style, stigma small, capitate. Fruit linear, apiculate with persistent style, 5–7 cm long, ca. 1.5 cm wide, light brown, glabrous, gynophore 5–10 mm long; seeds obovate, 7–10 mm long, 5–8 mm wide, surface dull, dark brown, funicular aril-lobe scars equal, forming an arcuate white line for ca. ⅘ the length of seed.

Bauhinia cookii is widespread species from Sinaloa in western Mexico southeast to Costa Rica. Collections have not been seen from Nicaragua, but it is to be expected there. It occurs in tropical deciduous or semideciduous forests at elevations from near sea level up to about 2,000 m but more commonly from 300 to 1,000 m. It apparently flowers throughout the year but most commonly from March to July. Flowers are sometimes produced before the leaves appear or are much developed.

This species is part of the Petiolata alliance but does not appear to be closely related to any of the other species of this alliance in Central America. It is easily recognized in Middle America because it is the only tree *Bauhinia* with light sulfur-yellow flowers in fasciculate clusters along the branches.

In Guatemala and El Salvador the local name is "Pata de Venado."

Representative specimens: MEXICO. CHIAPAS: Vicinity of La Chacona, *Miranda 6485* (US). COLIMA: Ca. 14 mi. WNW of Santiago on road to Cihuatlán, Jalisco, *McVaugh 20776* (MICH, US). GUERRERO: Cañón de la Mano Negra, near Iguala, *Rose et al. 9344* (F, GH, NY, US). JALISCO: Between Bahia Navidad and La Manzanilla on Bahia Tenacatita, 3 mi. W of Autlán-Navidad road, *McVaugh 21007* (MICH). NAYARIT: 7–8 mi. W of Compostela along road to Mazatan, *Gentry & Gilly 10848* (DUKE, MEXU, TEX). OAXACA: Ejido Benito Juárez, Sebástopol, Textepec, *Dioscorea Brigade 2741* (MEXU). SINALOA: Mazatlán, *Reko 4520* (MEXU, US). VERACRUZ: Municipio Puente Nacional, La Ceiba, *Ventura 12760* (MEXU). GUATEMALA. ESCUINTLA: Río Guacalate, *Standley 60187* (F, US). RETALHULEU: Río Talculán, 5 mi. W of Retalhuleu, *Standley 87377* (F). SUCHITEPÉQUEZ: Along Río Madre Vieja above Patulul, *Standley 62207* (F). HONDURAS. COMAYAGUA: Pito Solo, Lake Yojoa, *Edwards P-404* (F, US). COSTA RICA. ALAJUELA: Plains of the Río San Carlos, *Pittier 16695* (US). SAN JOSÉ: Cerro Bijaqualito-Tarcoles, *Póveda 1097* (MO).

6. Bauhinia coulteri Macbr., Contr. Gray Herb. 59: 22. 1919. Based on *Bauhinia platypetala* Benth. ex Hemsl.

Shrubs to 0.8 m or small tree up to 6 m tall; branches tomentose when young, soon glabrate. Leaves subcoriaceous, suborbicular, bilobate up to ⅓ their length, (2–)3–5(–6) cm long, (2–)3–5(–6) cm wide, base cordate, apex of lobes rounded, margins smooth to strongly crisped, upper surface glabrous, lower surface tomentose to glabrate, 5–9-nerved; petiole 1–2 cm long, slightly canaliculate, tomentose; stipules lanceolate, ca. 1 mm long, caducous; intrastipular excrescences minute. Inflorescences racemose, terminal, or subterminal and axillary, 2–10-flowered, rachis tomentose, buds narrowly lanceolate, 1.5–2.5 cm long, reddish tomentose, free tips ca. 1 mm long; bract narrowly lanceolate, 2.0–2.5 mm long; bracteoles similar but smaller than bract; pedicels slender, 1–2 cm long, tomentose; hypanthium cyathiform, 1–2 mm long; calyx spathaceous at anthesis; petals 5, subequal, pink or rarely white with darker venation, narrowly elliptic, sessile, (1–)2–3(–4) cm long, 0.5–1.5 cm wide, glabrous or strigulose near base on inner surface; fertile stamens 3, short-connate with staminodes, central stamen ca. ½ as long as petals, filament stout, anther oblong, ca. 2 mm long, glabrous, lateral stamens 5–7 mm long, filaments stout, glabrous, anthers as in central stamen; staminodes 7, subequal, 4–6 mm long, connate for ca. ½ their length, glabrous, abortive anthers present; pollen spheroid, 3-colporoidate, sexine reticulate; gynoecium ca. equalling petals, arcuate, strigose, gynophore subequalling style, stigma not much differentiated from style. Fruit linear, apiculate with persistent style, (5–)6–8(–15)

cm long, 1.0–1.5 cm wide, light brown, tomentellous to glabrate, gynophore ca. 1–2 cm long, tomentellous; seeds elliptic, 7–8 mm long, 4–5 mm wide, dark brown, funicular aril-lobe scars subequal, 2–3 mm long.

Two varieties are recognized.

KEY TO VARIETIES OF *BAUHINIA COULTERI*

1a. Shrubs up to 0.8 m tall; leaves subglabrous or sparsely pubescent below, margins smooth .... 6a. var. *coulteri*
1b. Small trees 5–6 m tall; leaves densely tomentose below, margins crisped .... 6b. var. *arborescens*

6a. Bauhinia coulteri Macbr. var. **coulteri**.

Bauhinia platypetala Benth. ex Hemsl., Diag. Pl. Nov. 49. 1880; non Burch. ex Benth., 1870. TYPE: Mexico. Hidalgo: Zimapán, *Coulter 531* (holotype, K; isotype, NY).
Casparia coulteri (Macbr.) Britt. & Rose, N. Amer. Fl. 23: 216. 1930.
Bauhinia coulteri forma *albiflora* Wunderlin, Rhodora 70: 286. 1968. TYPE: Mexico. Tamaulipas: 19 km SE of Miquihuana on road to Palmillas, *Stanford et al. 851* (holotype, MO; isotypes, GH, NY, UC).

Bauhinia coulteri is a central Mexican species of open oak-pine, juniper, or deciduous forests and occurs at elevations of 600 to 2,400 m. It flowers from April to September.

This species is easily recognized by its suborbicular leaves and pink (rarely white), sessile petals, and three fertile stamens. No other species of *Bauhinia* in Mexico has three fertile anthers. It is readily distinguished from var. *arborescens* by the characters given in the above key.

Representative specimens: MEXICO. HIDALGO: 16 km S of Jacala, *Frye & Frye 2251* (GH, MO, NY, UC, US). QUERÉTARO: 12 mi. E of Landa de Matamoros, *Crutchfield & Johnston 6136a* (TEX). SAN LUIS POTOSÍ: Minas de San Rafael, *Purpus 5187* (F, GH, MO, NY, P, UC, US). TAMAULIPAS: 18 mi. by road SE of Bustamante toward La Presita and Tula, *Johnston et al. 11154* (TEX).

6b. Bauhinia coulteri var. **arborescens** Wunderlin, Phytologia 15: 120. 1967. TYPE: Mexico. Querétaro: Ca. 80 km NE of Querétaro, above Pilón on road to Pinal de Arnoles, *McVaugh 10351* (holotype, MO; isotypes, DUKE, LL, MICH, TEX, US).

Bauhinia coulteri var. *arborescens* is known only from the type collection. It occurs in the lower limits of the pinyon pine-juniper belt at about 2,700 meters elevation. It was collected in flower in April.

This variety is easily distinguished from the typical by the characters in the above key.

The local name is "Manito de Cabra."

7. Bauhinia deserti (Britt. & Rose) Lundell, Publ. Carnegie Inst. Wash. no. 478. 211. 1937. *Casparia deserti* Britt. & Rose, N. Amer. Fl. 23: 216. 1930. *Bauhinia dipetala* var. *deserti* (Britt. & Rose) Wunderlin, Phytologia 15: 53. 1967. TYPE: Mexico. Puebla: Near Tehuacán, *Rose & Rose 11375* (holotype, US; isotype, NY).

Shrubs to 5 m tall; branches strigose or puberulent when young, soon glabrate. Leaves subcoriaceous, broadly ovate, bilobate ½ to ⅔ their length, lobes parallel or slightly divergent, (3–)5–8(–12) cm long, (3–)5–8(–12) cm wide, base cordate, apex of lobes rounded or obtuse, margins slightly crisped, upper surface glabrous, lower surface puberulent, 7–11-nerved; petiole 2–4 cm long, slightly canaliculate, puberulent; stipules ovate, 1.2–2.0 mm long, persistent; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 1.5 mm long, others minute. Inflorescences racemose, terminal, or subterminal and axillary, 20–30-flowered, rachis strigose, buds linear, 2–3 cm long, strigose, free tips up to 2 mm long; bract lanceolate, ca. 1.5 mm long; bracteoles similar to bract, but smaller; pedicels 0.6–15 mm long, strigose; hypanthium elongate-campanulate, 6–8 mm long; calyx spathaceous at anthesis; petals 2, subequal, linear, tapering to base, 1–2 cm long, brown pilose on inner surface; fertile stamen 1, 2.5–4.0 cm long, filament slender, arcuate, glabrous, short-connate with staminodes at base, anther linear-oblong, green, 8–12 mm long, glabrous; staminodes 9, subequal, 8–12 mm long, connate for ca. ¾ their length, brown pilose externally, abortive anthers absent; pollen spheroid, 3-colporoidate, sexine striato-reticulate with elongate supratectal processes; gynoecium ca. equalling stamen, arcuate, ovary tomentose, style and gynophore tomentellous, gynophore ca. equalling style, stigma subclavate, hardly differentiated from style. Fruit linear, apiculate with persistent style, 10–18 cm long, ca. 1 cm wide, dark brown, sparsely strigose, gynophore 2.5–3.5 cm long; seeds oblong, 8–10 cm long, 5–8 cm wide, surface dull, dark brown, funicular aril-lobe scars subequal, ca. 3 mm long.

Bauhinia deserti is restricted to the states of Oaxaca and Puebla in Mexico in dry deciduous forest at elevations of about 1,000 to 1,900 m

It apparently flowers throughout much of the year but most abundantly from August to November.

Bauhinia deserti is most closely related to *B. chapulhuacania* and *B. dipetala*; all three are characterized by green flowers with two petals. It is distinguished from *B. chapulhuacania* by its smaller leaves and fruits and from *B. dipetala* by its coriaceous leaves with the apex of the lobes usually rounded to obtuse. *Bauhinia deserti* is geographically separated from *B. chapulhuacania* and occurs in a dryer habitat than *B. dipetala. Bauhinia deserta* was reduced to a variety of *B. dipetala* by Wunderlin (1967) but examination of additional collections leads to the conclusion that it should be retained at the specific level.

This species is believed to be bat-pollinated, as are the related *B. chapulhuacania* and *B. dipetala*.

Representative specimens: MEXICO. OAXACA: Monte Albán, near Oaxaca, *Pringle 6065* (A, F, MO, MSC, NY, P, UC, US, VT). PUEBLA: Tehuacán, *Purpus 1190* (F, GH, MO, NY, UC).

8. **Bauhinia dipetala** Hemsl., Diag. Pl. Nov. 1880. *Casparia dipetala* (Hemsl.) Britt. & Rose, N. Amer. Fl. 23: 216. 1930. TYPE: Mexico. Veracruz: Valle de Córdoba, *Bourgeau 1713* (holotype, K; isotypes, F, GH, P, US).

Bauhinia unilateralis Britten & Baker, J. Bot. 35: 233. 1897. *Casparia unilateralis* (Britten & Baker) Britt. & Rose, N. Amer. Fl. 23: 214. 1930. TYPE: Mexico. Veracruz: Veracruz, *Houstoun s.n.* (holotype, BM).

Shrubs or small trees up to 5 m tall; branches strigose or puberulent when young, soon glabrate. Leaves chartaceous, broadly ovate, bilobate about ⅓, rarely to ½ their length, lobes parallel to slightly divergent, (3–)5–8(–12) cm long, (3–)5–8(–12) cm wide, base rounded to cordate, apex of lobes acute to obtuse, margins smooth or slightly crisped, upper surface glabrous, lower surface strigose or puberulent, 7–11-nerved; petiole 1.5–3.0 cm long, slightly canaliculate, strigose or puberulent; stipules lanceolate, ca. 1.5 mm long, persistent; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 1.5 mm long, others minute. Inflorescence racemose, terminal, or subterminal and axillary, 20–30-flowered, rachis strigose, buds linear, 1.0–1.5 mm long, strigose, free tips up to ca. 1 mm long; bract lanceolate, ca. 1.5 mm long; bracteoles similar to bract but smaller; pedicels ca. 5 mm long, strigose; hypanthium elongate-campanulate, 4–6 mm long; calyx spathaceous at anthesis; petals 2, subequal, linear, 6–8 mm long, ca. 2 mm wide, brown pilose on inner surface; fertile stamen 1, 2.0–2.5 cm long, filament slender, arcuate, glabrate, short-connate at base with staminodes, anther linear-oblong, green, 8–10 mm long, sparsely brown pilose, staminodes 9, subequal, 3–4 mm long, connate for ¾ or more their length, brown pilose on inner surface, abortive anthers absent; pollen spheroid, 3-colporoidate, sexine striato-reticulate with elongate supratectal processes; gynoecium ca. equalling stamen, arcuate, ovary tomentose, style and gynophore tomentellous to glabrate, gynophore ca. equalling style, stigma subclavate, hardly differentiated from style. Fruit linear, apiculate with persistent style, (8–)10–15(–18) cm long, 1.0–1.5 cm wide, dark brown, puberulent to glabrate, gynophore 2.0–2.5 cm long; seeds oblong, 7–8 mm long, 6–7 mm wide, surface dull, dark brown, funicular aril-lobe scars subequal, ca. 3 mm long.

Bauhinia dipetala occurs in southern Mexico and Belize along the edges of moist deciduous forest at elevations of 200 to 1,100 m. It has not been collected in Petén, Guatemala, but is to be expected there. It is sometimes cultivated as an ornamental and has become naturalized in Cuba. It flowers from December to May.

Bauhinia dipetala is most closely related to *B. deserti* and *B. chapulhuacania*, which also have green flowers with two petals.

The species has green flowers with a musky odor, which are bat-pollinated.

Representative specimens: MEXICO. CHIAPAS: Along a small river in the barrio of Tih Ha', paraje of Mahbenchauk, municipio of Tenejapa, *Ton 2050* (F, MSC, US). MORELOS: Oaxtepec, *Miranda 1209* (MEXU). OAXACA: Near Oaxaca, *Andrieux 2112* (P). PUEBLA: Tehuacán, *Diguet s.n.* (P). VERACRUZ: Ca. 10 mi. E of Córdoba, Highway 150, *Long & Burch 3125* (USF). BELIZE. CAYO: Banks of river above El Cayo, *Lundell 6136* (F, MICH, NY, TEX, US). CUBA. HAVANA: Near Havana, *León 6241* (NY).

9. **Bauhinia divaricata** L., Sp. Pl. 374. 1753; non Lam., 1785; nec Hort. ex Steud., 1840. *Mandarus divaricatus* (L.) Raf., Sylva Tellur. 122. 1838. *Casparia divaricata* (L.) H.B.K. ex Jackson in Index Kew. 1: 449. 1895, nom. inval. *Casparia divaricata* (L.) H.B.K. ex Britt. & Rose, N. Amer. Fl. 23: 215. 1930. TYPE: ?Jamaica: *Herb. Clifford* (holotype, BM).

Bauhinia divaricata [var.] *beta* L., Sp. Pl. ed. 2. 535. 1762. TYPE: ?Jamaica: *Herb. Miller* (holotype, BM).
Bauhinia aurita Ait., Hort. Kew. 2: 48. 1789. *Casparia aurita* (Ait.) Griseb., Fl. Brit. W. Ind. 213. 1860. Based on *Bauhinia divaricata* [var.] *beta* L.
Bauhinia divaricata Lam., Encyc. 1: 389. 1785; non L., 1753; nec Hort. ex Steud., 1840. TYPE: ?Jamaica: *Herb. Desfontaines* (holotype, FI, not seen).
Bauhinia porrecta Sw., Prodr. 66. 1788. *Casparia porrecta* (Sw.) Kunth ex Griseb., Fl. Brit. W. Ind. 213. 1860. *Casparia porrecta* (Sw.) H.B.K. ex Jackson in Index Kew. 1: 449. 1895, nom. inval. TYPE: ?Jamaica: *Swartz s.n.* (holotype, ?S, not seen).
Bauhinia latifolia Cav., Icon. 5: 4. 1799. *Casparia latifolia* (Cav.) H.B.K. ex Jackson in Index Kew. 1: 449. 1895, nom. inval. TYPE: Mexico: *Nee s.n.* (holotype, MA, not seen).
Bauhinia retusa Poir., Encyc. Suppl. 1: 599. 1811; non Ham. ex Roxb., 1832. TYPE: *Herb. Jussieu* (holotype, P-JU, not seen).
Bauhinia racemifera Desv., J. Bot. 3: 74. 1814. TYPE: America. *Herb. Desvaux* (holotype, P).
Bauhinia americana Laun., Herb. Amat. 5: t. 315. 1821. TYPE: Tropical America. *Herb. Launay* (holotype, P-JU, not seen).
Bauhinia lamarkiana DC., Prodr. 2: 512. 1825. Based on *Bauhinia divaricata* Lam.
Bauhinia spathacea DC., Prodr. 2: 512. 1825. *Casparia spathacea* (DC.) Britt. & Rose, N. Amer. Fl. 23: 211. 1930. TYPE: Based on a Sessé and Mociño plate (copy, G, not seen; photograph of copy at G, F, MO, US; blueprint of tracing of copy at G, MO, US).
Bauhinia furcata Desv., Ann. Sci. Nat. (Paris) 9: 429. 1826. *Casparia furcata* (Desv.) Jackson in Index Kew. 1: 449. 1895, nom. inval. TYPE: Tropical America. *Herb. Desvaux* (holotype, P).
Bauhinia adansoniana Guill. & Perr. Fl. Seneg. Tent. 1: 265. 1832. TYPE: The Adanson specimen is synonymous with *B. rufescens* Lam. of Africa but the description is of *B. divaricata* (fide Pellegrin, 1927).
Bauhinia versicolor Bertol., Hort. Bonon. Pl. Nov. 1: 7. 1838. *Casparia versicolor* (Bertol.) Britt. & Rose, N. Amer. Fl. 23: 215. 1930. TYPE: Mexico. Tamaulipas: Cultivated from seeds collected by Boschio, *Bertoloni s.n.* (holotype, BOLO, not seen).
Bauhinia mexicana Vog., Linnaea 13: 299. 1839. *Casparia mexicana* (Vog.) Britt. & Rose, N. Amer. Fl. 23: 214. 1930. TYPE: Mexico. Veracruz: Near Papantla, *Schiede s.n.* (holotype, B, not seen, presumed destroyed).
Bauhinia latifolia [var.] *beta* Hook. & Arn., Bot. Cap. Beech. Voy. 421. 1840. TYPE: Mexico. Nayarit: San Blas and Tepic, *Lay & Collie s.n.* (holotype, ?GL, not seen).
Bauhinia schlechtendaliana Mart. & Gal., Bull. Brux. 10: 308. 1843. *Casparia schlechtendaliana* (Mart. & Gal.) Britt. & Rose, N. Amer. Fl. 23: 215. 1930. TYPE: Mexico. Oaxaca: Río de las Vueltas, *Galeotti 3239* (holotype, BR, not seen; isotype, P).
Bauhinia amblyophylla Harms in Loess., Bull. Herb. Boissier 7: 548. 1899. *Casparia amblyophylla* (Harms) Britt. & Rose, N. Amer. Fl. 23: 211. 1930. LECTOTYPE: Mexico. Oaxaca: Between Tequisistlán and Jalapa, *Seler 1689* (NY). LECTOTYPE here designated; selected from syntypes: *Seler 1689* and *1890*, B, destroyed in World War II.
Bauhinia confusa Rose, Contr. U.S. Nat. Herb. 10: 97. 1906. *Casparia confusa* (Rose) Britt. & Rose, N. Amer. Fl. 23: 215. 1930. TYPE: Mexico. San Luis Potosí: Tomasopo Canyon, *Pringle 3104* (holotype, US; isotypes, CM, F, GH, MO, MSC, NY, UC, US, VT).
Bauhinia goldmanii Rose, Contr. U.S. Nat. Herb. 10: 97. 1906. TYPE: Mexico. Chiapas: Tuxtla Gutiérrez, *Goldman 742* (holotype, US; fragment of holotype, NY).
Bauhinia caribaea Jennings, Ann. Carnegie Mus. 11: 127. 1917. TYPE: Cuba. Havana: N of Caleta Grande, *Jennings 630* (holotype, CM).
Bauhinia peninsularis Brandeg., Univ. Calif. Publ. Bot. 10: 183. 1922. *Casparia peninsularis* (Brandeg.) Britt. & Rose, N. Amer. Fl. 23: 211. 1930. TYPE: Mexico. Baja California Sur: W side of Cape region, *Brandegee s.n.* (holotype, UC).
Bauhinia divaricata var. *angustiloba* Ekman ex Urban, Ark. Bot. 24A: 8. 1931. TYPE: Haiti. Sud: Massif de la Hotte, western group, Tiburón, in hills at Cap-à-faux, *Ekman 10535* (holotype, B, destroyed in World War II; isotypes, F, LL, NY, US).

Shrubs or small trees up to 8 m tall; branches strigose or tomentellous when young, soon glabrate. Leaves chartaceous to subcoriaceous, suborbicular to narrowly ovate to lanceolate, emarginate to bilobate about ¾, rarely nearly their entire length, lobes parallel or divaricate, 2–12 cm long, 2–10 cm wide, base rounded to cordate, apex of lobes acuminate to rounded, margins smooth to slightly crisped, upper surface tomentellous, puberulent, or glabrous, lower surface strigose or tomentellous, 5–9-nerved, petiole 0.5–4.0 cm long, slightly canaliculate, strigose, tomentellous, or glabrate; stipules ovate to linear, 1–3 mm long, deciduous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 2 mm long, others minute. Inflorescence racemose, terminal, or subterminal and axillary, (10–)20–50-flowered, rachis strigose or tomentellous, buds linear, 12–20 mm long, strigose or tomentellous, free tips up to 2 mm long; bract lanceolate to linear, 1.5–4.0 mm long; bracteoles similar to bract but smaller; pedicels 0.5–2.0 cm long, strigose or tomentellous; hypanthium cyathiform, 2–3 mm long; calyx spathaceous at anthesis; petals 5, subequal, white, turning pink in age, 1.5–2.5 cm long, blade ovate to narrowly elliptic, 1–3 times the length of claw, 1.5–6.0 mm wide, glabrous, claw glabrous; fertile stamen 1, subequalling to twice the length of petals, filament slender, slightly arcuate, glabrous, connate at base with staminodes, anther linear-oblong, ca. 2 mm long, black, glabrous;

staminodes 9, subequal, 1.0–1.5 cm long, connate for ¾ or more their length, white, petaloid, abortive anthers present or absent; pollen subspheroid, 3-colporoidate, sexine striate; gynoecium ca. equalling or slightly exceeding stamens, arcuate, short pilose to tomentose, ovary more pubescent than gynophore and style, gynophore ca. equalling style, stigma capitate, green. Fruit linear, apiculate with persistent style, 2.0–2.5 cm long, brown, puberulent to glabrate, gynophore 2.0–2.5 cm long; seeds oblong to suborbicular, 8–10 mm long, 6–8 mm wide, surface dull, dark brown, funicular aril-lobe scars subequal, ca. 3 mm long.

Bauhinia divaricata ranges from Baja California Sur east to Tamaulipas and south to Costa Rica in Middle America. It ranges throughout the Greater Antilles, except for Puerto Rico. It also occurs in St. Christopher and St. Thomas in the Lesser Antilles; its absence from Puerto Rico suggests that it is introduced there. It is the most common species of the genus in Mexico, Belize, northern Guatemala, and the Greater Antilles. *Bauhinia divaricata* occurs in a variety of habitats ranging from moist, open, deciduous forest to dry cactus scrub and is common in disturbed sites throughout its range. It ranges in elevation from near sea level up to 1,500 m but it is most commonly found from sea level to about 800 m. It flowers throughout the year but is affected by the availability of moisture, flowering most abundantly in the wet season.

Bahinia divaricata is most closely related to *B. rubeleruziana* of southwestern Mexico, Guatemala, and Belize from which it may be distinguished by white flowers, lack of dense yellowish-brown pubescence, and smaller leaves. *Bauhinia divaricata* probably originated in the southern Mexico and Guatemala area and from there spread north in Mexico, south to Costa Rica in Central America, and east in the Antilles as far as St. Christopher of the Lesser Antilles.

Bauhinia divaricata is highly polymorphic in leaf size, shape, and vesture. The flowers are also somewhat variable but much less so than the leaves. There are several geographic races that have been described as segregate species. However, these races intergrade considerably and no satisfactory method of distinguishing them taxonomically has been found. It seems best at this time to treat them as belonging to a single taxon.

In Mexico the local names for this species are "Pata de Cabra," "Pie de Cabra," "Pata de Vaca," "Pie de Vaca," "Ts'ulubtok'," and "Sakts'ulubtok'," in Belize "Pata de Vaca," "Pie de Vaca," "Bull Hoof," "Ts'ulubtok'," and in the Cayman Islands "Bull Hoof," in Jamaica "Bull Hoof" and "Mocco John," and in the Dominican Republic "Pata de Chivo" and "Huella de Chivo."

Representative specimens: MEXICO. BAJA CALIFORNIA SUR: Buena Vista, *Brandegee 177* (A, GH, US). CAMPECHE: Tuxpeña, *Lundell 962* (A, F, GH, MICH, MO, NY, UC, US, VT). CHIAPAS: 6 mi. SE of Chiapa de Corzo on Mexican Highway 190, *Raven & Breedlove 20140* (F, LL, MICH, NY, US). COLIMA: Ca. 11 mi. SSW of Colima on Manzanillo road, *McVaugh & Koelz 1598* (MICH, US). DURANGO: La Bajada, Tamazula, *Ortega 4397* (US). GUERRERO: Atoyoc, *Hinton et al. 10959* (F, GH, MICH, NY, P, UC, US). HIDALGO: Santa Ana, on Pan-American Highway, *Frye & Frye 2652* (GH, MO, NY, UC). JALISCO: 18–20 mi. SW of Autlán, *Gentry 10952* (MEXU, TEX). MICHOACÁN: Buena Vista, *Hinton et al. 12085* (F, IJ, LL, MICH, NY, P, UC, US). MORELOS: Cañón de Lobos, km 14 on Cuernavaca-Yautepec road, *Fryxell 764* (MO). NAYARIT: Vicinity of San Blas, *Ferris 5484* (A, US). OAXACA: Yaveo, N bank of Río Yaveo, *Mexia 9228* (F, GH, MO, NY, UC, US). PUEBLA: Near Matlaltayuca, *Goldman 52* (GH, US). QUERÉTARO: 74 mi. NE of Zimapán, *Waterfall & Wallis 14273* (TEX). QUINTANA ROO: Cozumel Island, vicinity of San Miguel de Cozumel, *Lewis 6856* (DUKE, MO); SAN LUIS POTOSÍ: 2 mi. W of Xilitla on road to Jalpán, *King 14308* (F, MICH, NY, TEX, UC, US). SINALOA: El Monte, near Los Labrodos, *Mexia 939* (A, GH, MICH, MO, NY, UC, US). TABASCO: Tenosique, *Matuda 3397* (A, F, LL, MICH, MO, NY). TAMAULIPAS: Vicinity of Ciudad Victoria, *Palmer 4* (CM, F, GH, MO, NY, UC). VERACRUZ: Near San Andrés Tuxtla, along river draining Laguna de Catemaca, *Dressler & Jones 232* (GH, MEXU, MICH, MO, NY, UC, US). YUCATÁN: Izamal, *Gaumer 336* (F, MO, NY, US, WIS). GUATEMALA. ALTA VERAPAZ: Along Río Sebol between Sebol and Carrizal, N of Sebol, *Steyermark 45765* (F, LL). CHIMALTENANGO: Chimaltenango, *Johnston 1735* (F). EL PROGRESO: Between Tululmajillo and Finca Montanita, *Steyermark 43343* (A, F). HUEHUETENANGO: Paso del Boqueron, along Río Trapichillo, below La Libertad, *Steyermark 51130* (F). PETÉN: Vaxactun, *Bartlett 12511* (MICH, NY, UC, US). RATALHULEU: Between Nueva Linda and Champerico, *Standley 87623* (F). ZACAPA: *Kellerman 7875* (F, NY, UC, US). BELIZE. BELIZE: Near Gracie Rock, *Wunderlin 5022* (MO). CAYO: 41 mi. section, Belize-Cayo Road, *Gentle 9692* (F, IJ, MICH, TEX, UC, US). COROZAL: Adventura, *Gentle 4745* (MICH, NY, UC). ORANGE WALK: Honey Camp, *Lundell 640* (A, F, GH, MO, NY, UC, US). STANN CREEK: Stann Creek Railway, *Schipp 221* (A, F, GH, MICH, MO, UC). TOLEDO: Forest Home, *Schipp 8502* (F). HONDURAS. ATLANTIDA: Vicinity of La Ceiba, *Yuncker et al. 8801* (F, GH, MICH, MO, NY, UC, US). COPÁN: Along Río Copán near Copán ruins, *Molina 6624* (F, US). CORTÉS: Near La Lima, *Williams & Molina 12454* (F, GH, MICH). EL PARAÍSO: Along the Río Guayambre, Valle Jamastrán, *Molina 7367* (F). FRANCISCO MORAZÁN: Quebrada Contarranas, NE of Contarranas, *Molina 7808* (F, US). SANTA BÁRBARA: San Pedro Sula,

Thieme 5183 (GH, NY, US). OLANCHO: Vicinity of Catacamas, *Standley 18410* (F). YORO: Agua Blanca, 10 mi. S of Progreso, *Record & Kuylen H.35* (GH, NY, US). EL SALVADOR. SONSONATE: Near Yuayua, *Pittier 1988* (NY, US). NICARAGUA. MATAGALPA: El Tuma, 30 km E of Matagalpa, *Neill 2351* (MO, USF). RIVAS: Along road SE of San Juan del Sur at Río La Flor, *Stevens 3822* (MO, USF). COSTA RICA. GUANACASTE: Ca. 11 km N of La Cruz, 0.5 mi. W of main road, *Liesner 4851* (MO, USF). CUBA. HAVANA: Isla de Pinos, Caleta Crocodrilos, *Britton et al. 15316* (NY). MATANZAS: Península de Zapata, *Ekman 18346* (F, MICH, MO, P, UC, US). PINAR DEL RÍO: Río Portales, *Shafer 11168* (F, MO, NY, US). CAYMAN ISLANDS. Little Cayman, near Snipe Point, *Proctor 28040* (IJ, LL). JAMAICA. CLARENDON: Near Salt River, *Wedderburn 267* (IJ). HANOVER: 2.2 mi. W of Sandy Bay, *Wunderlin 5097* (MO, USF). MANCHESTER: Vicinity of Mandeville, *Crawford 735* (NY, US). PORTLAND: Port Antonio, *Hitchcock s.n.* (MO, US). ST. ANDREW: Northern end of Long Mountain, just E of Kingston, *Crosby et al. 106* (DUKE, F, LL, MICH, MO, MSC, NY, UC, US, USF). ST. ANN: 1 mi. S of Boscobel, *Proctor 6624* (IJ, LL, US). ST. CATHERINE: Rodney's Lookout near Port Henderson, *Wunderlin 5073* (MO, USF). ST. ELIZABETH: Near Ipswich, *Maxon & Killip 1501* (F, ILL, US). ST. JAMES: Orange River, near Montego Bay, *Maxon & Killip 1668* (F, ILL, US). ST. THOMAS: Along road between Holland Bay and Morant Point, *Proctor 27843* (IJ, LL, MICH, US). TRELAWNY: Road N of Spring Garden toward Burnt Hill, *Anderson & Sternberg 1239* (DUKE, LL, MO, US). HAITI. GONAVE ISLAND: Vicinity of Etroite, *Leonard 3283* (NY, US). L'ARTIBONITE: Vicinity of Ennery, *Leonard 9470* (MO, US). NORD: Vicinity of St. Michel de L'Atalaye, *Leonard 7337* (F, NY, UC, US). OESTE: Near Turgeu Springs, Port-au-Prince, *Holdridge 985* (F, MICH, NY, TEX, US). SUD: Miragonne and vicinity, *Eyerdam 479* (F, MO, US). DOMINICAN REPUBLIC. AZUA: *Rose et al. 3955* (F, NY, US). BARAHONA: Montiada Nueva SE of Polo, *Howard & Howard* (MICH, NY, P, US). PEDERNALES: Banano, *Marcano 5248* (NY). ST. CHRISTOPHER. *Masson s.n.* (photograph of specimen at BM, IJ). ST. THOMAS. *Reidle s.n.* (P).

10. **Bauhinia erythrocalyx** Wunderlin, Sida 5: 353. 1974. TYPE: Mexico. Campeche: "Central Buenfil" (?Puerto Buen Fiel), *Lundell 1152* (holotype, F; isotypes, F, MICH).

Bauhinia petensis Lundell, Wrightia 5: 344. 1977. TYPE: Guatemala. Petén: Dos Lagunas, 1 km N of village, *Lundell & Contreras 20475* (holotype, LL, not seen; isotype, LL).

Shrubs or small trees up to 15 m tall; branches strigose when young, soon glabrate. Leaves chartaceous, ovate, bilobate for ½ their length, lobes divergent, 3.5–7.0 cm long, 4–6 cm wide, base cordate, apex of lobes obtuse, margins slightly crisped, upper surface glabrous, lower surface strigose, 7-nerved; petiole 1.5–3.0 cm long, slightly canaliculate, strigose; stipules lanceolate, ca. 1.5 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection ca. 1.5 mm long, others minute. Inflorescences racemose, terminal, or subterminal and axillary, 10–20-flowered, rachis strigose, buds linear, 1.5–2.0 cm long, strigose, red, free tips minute; bract ovate-lanceolate, ca. 1 mm long; bracteoles similar to and slightly smaller than bract; pedicels 1–2 cm long, strigose, reddish; hypanthium cyathiform, 2–3 mm long; calyx spathaceous at anthesis; petals 5, subequal, white or cream, ca. 1.5 cm long, blade linear-lanceolate to oblanceolate, ca. ⅓ the length of claw, 2–3 mm wide, sparsely pilose externally, claw glabrate; fertile stamen 1, slightly exceeding the petals, filament slender, slightly arcuate, glabrous, connate with staminodes at base, anther oblong, 3–4 mm long, red, glabrate; staminodes 9, alternate staminodes slightly shorter, 1.0–1.5 cm long, connate for ca. ½ their length, pilose on inner surface at connate portion, abortive anthers present or absent; pollen peroblate, 3-colporoidate, reticulate; gynoecium subequalling fertile stamen, slightly arcuate, ovary densely strigose, gynophore and style sparsely and loosely strigose, gynophore subequalling style, stigma slightly differentiated from style. Fruit linear, apiculate with persistent style, 7–10 cm long, ca. 1.5 cm wide, light brown, strigose to glabrate, gynophore ca. 2 cm long, glabrate; seeds oblong, 4–6 mm wide, dark brown, funicular aril-lobe scars subequal, ca. 1.5 mm long.

Bauhinia erythrocalyx is a rare species occurring in Campeche, Quintana Roo, and Yucatán, Mexico and adjacent Petén, Guatemala. It occurs in dry, often rocky, semideciduous forests at elevations from near sea level up to about 400 meters.

Bauhinia erythrocalyx is most closely related to *B. jenningsii*, a more common and widespread species occurring in the same general area. It is readily distinguished from *B. jenningsii* by its bilobate leaves.

Specimens examined: MEXICO. CAMPECHE: Near Xpujil, *Shepherd 16* (LL, WIS). YUCATÁN: 8 km W of Xpujil, *Waide s.n.* (WIS); Mérida, *Novelo 404* (US). QUINTANA ROO: 44 km S of Escárcega-Chetumal highway on road to Icaiché, *Guero & Grether 909* (MO); 5 km from the Chetumal-San Carillo Puerto highway on road to El Placer, *Téllez & Cabrero 1277* (MO). GUATEMALA. PETÉN: Dos Lagunas, bordering the North Lake, *Contreras 1660* (LL).

FIGURE 1. *Bauhinia fryxellii.* A. Flowering branch. B. Flower (×1.3).

11. Bauhinia fryxellii Wunderlin, sp. nov., fig. 1. TYPE: Mexico. San Luis Potosí: Municipio Ciudad Valles, Rancho Pago Pago, 3.5 mi. by road W of Chantol, near juncture of Río Mesillas and Río Mico, *Fryxell & Anderson 3427* (holotype, USF; isotypes, to be deposited in CHAPA, ENCB, K, MO, MEXU, MICH, pf, TEX, US). ("pf" is the personal herbarium of Paul Fryxell.)

Bauhinia jucunda Brandeg. affinis, a qua imprimis differt foliis majoribus magis profunde lobatus, stylo breviori, et filamento staminis fertilis piloso ad basim.

Shrub to 1 m tall; branches sparsely puberulent-strigose when young, soon glabrate. Leaves chartaceous, bilobate ⅘ or more their length, lobes narrowly elliptic-lanceolate, divergent, slightly arcuate, 8–11 cm long, 2.2–2.8 cm wide, base rounded, apex of lobes rounded, margins smooth or slightly crisped, upper surface bright green, glabrous, lower surface paler, minutely strigose, lobes 1–3-nerved; petiole 2.5–3.0 cm long, slender, slightly canaliculate, sparsely puberulent-strigose; stipules ovate, aristate tipped, ca. 2 mm long, caducous; adpetiolar intrastipular excrescence elongated and forming a flattened, slightly antrorsely arcuate spine ca. 2 mm long, others minute. Inflorescences short-racemose, axillary, 6-flowered, rachis sparsely strigose; buds linear, ca. 1.7 cm long, sparsely strigose, free tips obsolete; bract lanceolate, ca. 1.5 mm long, strigose; bracteoles similar to bract but slightly shorter; pedicels 3–4 mm long, strigose; hypanthium short tubular-campanulate, ca. 6 mm long; calyx spathaceous at anthesis, green; petals 2, only 1 well developed, linear, greenish-white, up to 1 cm long, pilose on inner surface, the smaller one up to 5 mm long or reduced to a short filament, rarely with a third vestigial petal; fertile stamen 1, 2.0–2.3 cm long, short-connate at base with staminodes, filament ca. 1.8 cm long, pilose on lower ⅓, anther linear-oblong, 7–8 mm long, sparsely pilose on ventral surface; staminodes 9, united by their flattened filaments ¼ to ¾ their length, longest adjacent to fertile stamen ca. 8 mm long, shortest ca. 5 mm long, all without vestigial anthers, outer surface of staminal tube and free filaments pilose nearly to base, inner surface pilose only on upper part; pollen spheroid, 3-colporoidate, sexine striato-reticulate with elongate supratectal processes; gynoecium ca. 1.8 cm long, linear; ovary short stipitate, appressed pubescent, stipe ca. 5 mm long, strigose; style ca. 5 mm long, sparsely pilose, stigma capitate. Fruit linear-oblong, apiculate with persistent style, 6–7 cm long, dark brown, sparsely strigose, gynophore ca. 1 cm long; seeds subquadrangular, 7–8 mm long, 4–6 mm wide, surface shiny, reddish-brown, funicular aril-lobe scars subequal, ca. 1.5 mm long.

Bauhinia fryxellii is a rare species known only from the type collection. It was collected at 110 meters elevation in a cut-over field. Collected in May, it was in flowering and fruiting condition.

Bauhinia fryxellii belongs to an alliance of five species that includes *B. chapulhuacania, B. deserti, B. dipetala,* and *B. jucunda.* This group differs from all other monandrous Neotropical species of *Bauhinia* in that they have a reduced number of petals, usually 2, rarely 1, 3, or 4. *Bauhinia fryxellii* is most closely allied to *B. jucunda* but differs in its larger, more deeply lobed leaves, shorter style, and the filament of the fertile stamen pilose near base.

The species is named in honor of one of its collectors, the noted student of Malvaceae, Paul A. Fryxell.

12. Bauhinia jenningsii P. Wilson in Britt., Bull. Torrey Bot. Club 43: 463. 1916. *Casparia jenningsii* (P. Wilson) Britt. & Rose, N. Amer. Fl. 23: 216. 1930. TYPE: Cuba. Havana: Isle de Pinos, Coe's Camp, Ensenada de Siguanea, *Britton & Wilson 14851* (holotype, NY; isotypes, CM, F, MO, NY, P, US).

Bauhinia castilloi Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 78. 1940. TYPE: Belize. Stann Creek: Freshwater Creek Reserve, *Castillo 48* (holotype, F).

Slender shrub or small tree to 6 m tall; branches glabrate. Leaves subcoriaceous, ovate to lanceolate, 7–14 cm long, 2.5–5.0 cm wide, apex acuminate to obtuse, base truncate to rounded, upper surface bright green, glabrous, lower surface lighter in color, strigulose to glabrate, 5-nerved; petioles 1.5–2.0 cm long, terete or slightly canaliculate, glabrate; stipules lanceolate, ca. 1.5 mm long, caducous, adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 1.5 mm long, others minute. Inflorescences racemose, terminal or subterminal and axillary, 10–30-flowered, rachis loosely strigose, reddish; buds linear, 1.5–2.0 cm long, loosely strigose, red, free tips minute; bract lanceolate, ca. 0.5 mm long; bracteoles similar to bracts but slightly shorter; pedicels slender, 1.0–1.5 cm long, loosely strigose, reddish; hypanthium cyathiform, 2-

3 mm long; calyx spathaceous at anthesis; petals 5, subequal, white or cream, 1.2–2.0 cm long, blade linear-lanceolate to oblanceolate, subequalling claw, 2–3 mm wide, sparsely pilose externally, claw glabrate; fertile stamen 1, slightly exceeding the petals, filament 1.5–2.0 cm long, slender, slightly arcuate, glabrous, short-connate with staminodes at base, anther linear-oblong, 4–5 mm long, glabrous, staminodes 9, 1.0–1.5 cm long, alternate slightly shorter, connate for ca. ⅓ their length, sparsely pilose on inner surface at connate portion, aborted anthers present; pollen peroblate, 3-colporoidate, sexine reticulate; gynoecium subequalling fertile stamen, slightly arcuate, ovary densely pilose, gynophore and style sparsely pilose, gynophore subequalling style, stigma not much differentiated from style. Fruit linear, apiculate with persistent style, 5–10 cm long, 1–2 cm wide, light brown, strigulose, gynophore ca. 2 cm long, glabrous; seeds oblong, 7–9 mm long, 5–7 mm wide, dark brown, funicular aril-lobe scars equal, ca. 2.5 mm long.

An uncommon species occurring in Cuba, the Yucatán Peninsula of Mexico, Belize, and northern Guatemala. It occurs in rocky, calcareous soils along the edge of dry to mesic or sometimes moist woods. It flowers from February to September.

Bauhinia jenningsii is a unique species, readily distinguished from other *Bauhinia* species within its range by its entire, *Smilax*-like leaves. It is most closely related to *B. erythrocalyx* of the Yucatán Peninsula. The flowers of the two species are very similar, but *B. jenningsii* differs in its entire leaf.

The local name for this species in Belize is "Cow Tongue" and the Mayan name in Mexico is "Chakts'ulubtok'."

Representive specimens: MEXICO. QUINTANA ROO: 3–4 mi. S of Filipe Carrillo Puerto, *Wunderlin 5020* (MO, USF). YUCATÁN: Puerto Morelos, *Goldman 624* (NY, US). GUATEMALA. PETÉN: Vaxactun, *Bartlett 12145* (MICH, NY, UC, US). BELIZE. CAYO: Vaca, *Gentle 2271* (MICH). CUBA. HAVANA: Isla de Pinos, San Juan, *Britton et al. 15544* (CM, F, MO, NY, US).

13. **Bauhinia jucunda** Brandeg., Univ. Calif. Publ. Bot. 7: 326. 1920. *Casparia jucunda* (Brandeg.) Britt. & Rose, N. Amer. Fl. 23: 213. 1930. TYPE: Mexico. Veracruz: Barranca de Pancava, *Brandegee 8535* (holotype, UC).

Shrubs to 2 m tall; branches strigose when young, soon glabrate. Leaves chartaceous, bilobate for ½ or more their length, lobes lanceolate or triangular, divaricate, 5–8 cm long, 3–5 cm wide at base, 5–8 cm wide between lobes at tips, base cordate to truncate, apex of lobes obtuse, margins moderately crisped, upper surface glabrous, lower surface strigulose to glabrate, 5-nerved; petiole 1–2 cm long, slightly canaliculate, strigose; stipules lanceolate, ca. 1.5 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to ca. 1.5 mm long, other minute. Inflorescences racemose, terminal, or subterminal and axillary, 10–30-flowered, rachis strigulose, buds linear, 1.5–2.0 cm long, strigose, free tips minute; bract lanceolate, ca. 1.5 mm long; bracteoles similar, but smaller than bract; pedicels 0.5–1.2 cm long, strigose; hypanthium cyathiform, 3–5 mm long; calyx spathaceous at anthesis; petals usually 3, rarely 2 or 4, sometimes third and/or fourth represented only by a filament or obsolete, rarely a fifth vestigial petal present, white, linear, 1.0–1.5 cm long when fully developed, blade linear, 2–4 times longer than claw, densely pilose, ca. 1.5 mm wide, claw densely pilose; fertile stamen 1, ca. 1 cm longer than petals, filament slender, slightly arcuate, glabrous, slightly connate at base with staminodes, anther oblong, ca. 1 cm long, sparsely pilose; staminodes 9, 5–8 mm long, connate for ½ or more their length, pilose, abortive anthers absent; pollen spheroid, 3-colporoidate, sexine striato-reticulate with elongate supratectal processes; gynoecium subequalling fertile stamen, slightly arcuate, ovary tomentose, gynophore and style tomentellous, gynophore subequalling style, stigma capitate, slightly oblique. Fruit linear, apiculate with persistent style, 8–10 cm long, ca. 1 cm wide, brown-strigose, gynophore ca. 1 cm long, glabrate; seeds oblong, 6–8 mm long, 4–6 mm wide, surface dull, brown, funicular aril-lobe scars equal, ca. 1 mm long.

Bauhinia jucunda is a rare species endemic to a small area in eastern Veracruz, Mexico, and known from only a few collections. It occurs in low, deciduous forests at 200–500 m. It apparently flowers from July to November, rarely as early as April.

This species belongs to an alliance of five species that includes *B. chapulhuacania, B. deserti, B. dipetala,* and *B. fryxellii.* This species differ from other monandrous Neotropical species of *Bauhinia* in having a reduced number of petals, usually 2, rarely 1, 3, or 4. *Bauhinia jucunda* is most closely related to *B. fryxellii,* but differs in having

smaller, less deeply lobed leaves, a longer style, and a glabrous filament of the fertile stamen.

Specimens examined: MEXICO. VERACRUZ: Road from Xalapa on detour to Los Banos de Carrizal Emiliano Zapata, *Calzada 2043* (F, MEXU, USF); Plan del Río, Municipio Dos Ríos, *Ventura 5787* (MEXU, NY); *8994* (MEXU); La Ceiba, Municipio Puente Nacional, *Ventura 12061* (MEXU); Remudadera, *Purpus 8833* (GH, NY); *8986* (F, GH, MO, NY, UC, US); without precise locality, *Purpus 8940* (UC).

14. Bauhinia lunarioides A. Gray ex S. Wats., Bibl. Ind. N. Amer. Bot. 205. 1878. TYPE: Mexico. Coahuila: Rocky hills near Santa Rosa, *Perry 2901A* (holotype, GH).

Casparia congesta Britt. & Rose, N. Amer. Fl. 23: 211. 1930. *Bauhinia congesta* (Britt. & Rose) Lundell, Phytologia 1: 214. 1937. TYPE: Mexico. Coahuila: Mountains 24 mi. NE by N from Monclova, *Palmer 285* (holotype, US; isotypes, LE, NY, P, VT).

Casparia jermyana Britt. in Britt. & Rose, N. Amer. Fl. 23: 211. 1930. *Bauhinia jermyana* (Britt.) Lundell, Phytologia 1: 214. 1937. TYPE: United States. Texas: Gillespie Co.: Enchanted Rock, *Jermy s.n.* (holotype, NY). [See discussion below.]

Shrub up to 4 m tall; branches loosely strigose when young, soon glabrate. Leaves subcoriaceous, broadly ovate to suborbicular, bilobate for ¾ or more their length, usually bifoliolate, lobes suborbicular, slightly divergent, inner margins straight to slightly convex, (1.0–)1.5–2.5(–3.0) cm long, (1.5–)2.0–2.5(–3.0) cm wide, base cordate or rarely truncate, apex of lobes rounded, margins slightly to moderately crisped, upper surface glabrous, lower surface strigose to glabrate, (5–) 11-nerved; petiole 0.5–1.0(–1.5) cm long, slightly canaliculate, loosely strigose; stipules broadly lanceolate, ca. 1 mm long, caducous; intrastipular excrescences minute. Inflorescences short racemose, terminal, or subterminal, 2–6(–10)-flowered, rachis strigose, buds narrowly lanceolate, 1–2 cm long, loosely strigose with white hairs, occasionally purplish-tinged, free tips ca. 2 mm long; bract lanceolate, ca. 1 mm long; bracteoles similar but smaller than bract; pedicels slender, 0.5–1.0 cm long, strigose; hypanthium cyathiform, 1–2 mm long; calyx spathaceous at anthesis; petals 5, subequal, white or occasionally pinkish-tinged, 1.5–2.5 cm long, blade elliptic-lanceolate to ovate, ca. 3 times the length of claw, 0.7–1.2 cm wide, glabrous to sparsely pilose on inner surface, claw pilose to glabrate; fertile stamen 1, subequalling petals, filament slender, slightly arcuate, sparsely pilose at base, short-connate with staminodes, anther oblong, 5–7 mm long, glabrous; staminodes 9, subequal, 5–7 mm long, connate for ca. ½ their length, pilose below, rarely glabrous, abortive anthers usually present; pollen spheroid, 3-colporoidate, sexine striato-reticulate; gynoecium subequalling petals, slightly arcuate, gynophore ca. ½ the length of style, gynophore and ovary pilose, stigma capitate, bilobate, dark in contrast with style. Fruit linear, apiculate with persistent style, 5–8 cm long, 1–2 cm wide, light brown, glabrate, gynophore ca. 5 mm long, strigose; seeds 7–10 mm long, 6–8 mm wide, surface dull, dark brown, funicular aril-lobe scars unequal, one ca. 1.5 mm long, other ca. 0.5 mm long.

Bauhinia lunarioides is restricted to Coahuila and Nuevo León, Mexico, and adjacent Texas. It occurs in desert scrub, primarily on calcareous soils at elevations of 500 to 2,00 m. It flowers primarily from March to June.

There is considerable debate concerning the distribution of this species in Texas. In addition to the several collections from the Anacacho Hills, Kinney County, by various collectors, single collections have been seen that, according to the label data, are from Gillespie (type of *Casparia jermyana*), Maverick, Presidio, Val Verde, and Webb counties. However, B. L. Turner and M. C. Johnston (pers. comm.) suspect that the label information for these collections is incorrect and that all Texas material is actually from the Anacacho Hills. The occurrence of the species in Texas in these counties, with the exception of Gillespie (see below), is logical and these herbarium records cannot be completely disregarded. However, not having personally verified the occurrence of the species at the reported localities in southern Texas, I reserve judgement on this point.

The type collection of *Casparia jermyana* Britt. is stated in the protolog and on the label of the holotype specimen to have come from Enchanted Rock, Gillespie County, Texas. However, this is probably an error since recent work has failed to produce any species of *Bauhinia* at Enchanted Rock. Furthermore, *B. lunarioides* grows primarily on calcareous soils and Enchanted Rock is a granite outcrop. It is possible that the collection is actually from the Anacacho Mountains in Kinney County where it is well known.

Bauhinia lunarioides is readily distinguished from the other white-flowered monandrous species of *Bauhinia* by its usually bifoliolate

leaves. Other species within the range of *B. lunarioides* that may occasionally have bifoliolate leaves have purple to pink flowers. It is probably most closely related to *B. divaricata* but is more northern and xerophilous than that species.

Representative specimens: UNITED STATES. TEXAS: Kinney Co.: Anacacho Ranch, SW slopes of Anacacho Mountains, *Correll & Rollins 32537* (FSU, TEX, UC, US). Maverick Co.: Near Eagle Pass, *Tharp 44159* (TEX). Presidio Co.: *Jermy s.n.* (MO). Val Verde Co.: SW side of the Devil's River, 0.25–0.5 mi. NW of confluence of the Devil's River and Dolan Creek, *Smith & Butterwick 166* (LL). Webb Co.: Near Laredo, *Warnock s.n.* (TEX). MEXICO. COAHUILA: San Lázaro, near the northern entrance of El Puerto de San Lázaro, *Wynd & Mueller 109* (A, ILL, MICH, MO, MSC, NY, US). NUEVO LEÓN: 8 mi. W of Monterrey on way to Saltillo, *Hitchcock & Stanford 6835* (NY, UC, US).

15. **Bauhinia macranthera** Benth. ex Hemsl., Diag. Pl. Nov. 49. 1880. *Casparia macranthera* (Benth. ex Hemsl.) Britt. & Rose, N. Amer. Fl. 23: 212. 1930. TYPE: Mexico. Hidalgo: Zimapán, *Coulter s.n.* (holotype, K).

Bauhinia retifolia Standl., Contr. U.S. Nat. Herb. 23: 416. 1922. *Casparia retifolia* (Standl.) Britt. & Rose, N. Amer. Fl. 23: 213. 1930. TYPE: Mexico. San Luis Potosí: Rascón, *Purpus 5268* (holotype, US; isotypes, F, MEXU, MO, NY, UC).

Casparia lunarioides A. Gray ex Britt. & Rose, N. Amer. Fl. 23: 212. 1930. TYPE: Mexico. Nuevo León: Sierra de la Silla, Monterrey, *Pringle 2529* (holotype, US; isotypes, A, CM, F, GH, MO, MSC, NY, P, UC, VT).

Bauhinia macranthera var. *grayana* Wunderlin, Phytologia 15: 53. 1967. Based on *Casparia lunarioides* A. Gray ex Britt. & Rose.

Shrub or small tree up to 4(–7) m tall; branches strigose or tomentose when young, soon glabrate. Leaves subcoriaceous, ovate, bilobate for ½ to ¾ their length, rarely bifoliolate or lobed less than ½ their length, lobes parallel or slightly divergent, (3–)5–7(–11) cm long, (3.5–)5–8(–9) cm wide, base cordate, apex of lobes rounded to obtuse, margins slightly to strongly crisped, upper surface glabrous, lower surface strigose, pilose, or glabrate, 7–9(–11)-nerved; petiole 1.5–2.5(–4.0) cm long, slightly canaliculate, tomentose, strigose, or glabrate; stipules linear-lanceolate, ca. 2 mm long, caducous; intrastipular excrescences minute; inflorescences short-racemose, subterminal, axillary, 3–10-flowered, rachis strigose or tomentose, buds narrowly lanceolate, 2.0–2.5(–3.0) cm long, strigose or tomentellous, free tips setaceous, (2–)3–6(–10) mm long; bract linear-lanceolate, 1.5–2.0 mm long; bracteoles similar but smaller than bract; pedicels 3–6 mm long, strigose or tomentose; hypanthium cyathiform, 1–2 mm long; calyx spathaceous at anthesis; petals 5, subequal, pink to purple darker-veined, (2.5–)3.0–3.5(–4.0) cm long, blade obovate to elliptic, subequalling length of the pilose claw, 0.5–1.0 cm wide, glabrous or sparsely pilose at base; fertile stamen 1, ca. ¾ the length of petals, filament stout, arcuate, pilose at base, short-connate with staminodes, anther oblong, 7–9 mm long, sparsely pilose; staminodes 9, subequal, 6–8 mm long, connate ca. ½ their length, pilose below, abortive anthers present or absent; pollen spheroid, 3-colporoidate, sexine striato-reticulate; gynoecium subequalling petals, arcuate, densely pilose, gynophore subequalling style, stigma oblique, slightly differentiated from style. Fruit linear, apiculate with persistent style, (6–)8–12(–15) cm long, 1–2 cm wide, light brown, tomentose to glabrate, gynophore 1.0–1.5 cm long, glabrate; seeds oblong, 8–12 mm long, 6–8 mm wide, surface shiny, brown, funicular aril-lobe scars equal, ca. 4 mm long.

Bauhinia macranthera occurs in central and northeastern Mexico in open, deciduous forests at elevations ranging from 600 to 2,500 m. It flowers from March to August.

The closest relative to *B. macranthera* and that with which it has been confused is *B. ramosissima.* It is distinguished from that species by usually pink rather than purple flowers, larger, usually bilobate rather than bifoliolate leaves, and setaceous calyx tips.

Representative specimens: MEXICO. COAHUILA: Rancho Agua Dulce, lower slopes of the Sierra de San Miguel, *Wynd & Mueller 316* (A, ILL, MICH, MO, MSC, NY, US). HIDALGO: Puente de la Zorra, near Km 284 on highway NE of Jacala, *Moore 1711* (GH, UC, US). NUEVO LEÓN: Sierra Madre Oriental, waterway below Alamar, ca. 15 mi. SW of Galeana, *Mueller & Mueller 654* (A, F, MICH, NY, P, TEX, US). SAN LUIS POTOSÍ: Ca. 10 mi. NE of Ciudad del Maiz (17 mi. by road), *McVaugh 10434* (DUKE, GH, LL, MICH, MO, TEX, US). TAMAULIPAS: Along route 70, ca. 11 mi. S of Ciudad Victoria, *King 4552* (F, MICH, NY, TEX, UC, US). VERACRUZ: E of Rinconada, *Gregg 760* (MO, NY).

16. **Bauhinia multinervia** (H.B.K.) DC., Prodr. 2: 515. 1825. *Pauletia multinervia* H.B.K., Nov. Gen. Sp. Pl. 6: 316. 1825. TYPE: Venezuela. "Prope Caracas, Caripe et Montana de Capaya," *Humboldt & Bonpland 576* (holotype, P; microfiche, MO; isotype B(W); photographs of isotype at B(W), F, MO, US).

Pauletia glaucescens H.B.K., Nov. Gen. Sp. Pl. 6: 317. 1823. *Bauhinia glaucescens* (H.B.K.) DC., Prodr. 2: 515. 1825. TYPE: Venezuela. Sucre: *Humboldt & Bonpland 221* (holotype, P; microfiche, MO).
Bauhinia megalandra Griseb., Fl. Brit. W. Ind. 213. 1860. LECTOTYPE: St. Vincent: *Guilding s.n.* (lectotype, K; photographs of lectotype, F, IJ, US). Lectotype here designated.

Large shrub or small tree up to 10 m tall; branches ferruginous puberulent when young, soon glabrate. Leaves chartaceous, suborbicular to oblong, bilobate for ca. ½ their length, 7–15 cm long, 6–14 cm wide, base cordate to rounded, apex of lobes rounded, upper surface glabrous, lower surface glabrate or occasionally glaucous, ferruginous puberulent on nerves, (5–)7–9 (–11)-nerved; petioles 2–4 cm long, canaliculate, ferruginous pubescent or glabrate; stipules ovate, ca. 2 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 1.5 mm long, others minute. Inflorescences racemose or paniculate through reduction of subterminal leaves opposite single flowers, up to 20-flowered, rachis ferruginous puberulent to velutinous, buds linear, 6–8 cm long, ca. 1 cm thick, ferruginous velutinous, apex rounded; bract triangular, ca. 1 mm long; bractioles similar to bract; peduncle 1–3 cm long, ferruginous puberulent or velutinous; hypanthium tubular, 2–3 cm long; calyx splitting into 5 lobes or lobes partly connate, curled and reflexed at anthesis, pale green on inner surface; petals 5, subequal, white, filiform, 8–12 cm long, 3–5 mm wide; fertile stamens 10, equalling or exceeding petals, alternate ones slightly shorter, slightly spreading, filaments slender, white, short-connate at base for ca. 1 cm, puberulent toward base and on inner surface, anthers 1.5–2.0 cm long, glabrous; pollen spheroid, 3–6-poroidate, sexine reticulate with blunt, spinelike infratectal processes; gynoecium subequalling stamens, ovary and gynophore purple, puberulent, style glabrate in upper ½, greenish-white, gynophore subequalling style, stigma oblique. Fruit linear, apiculate with persistent style, 15–20 cm long, 2.0–2.5 cm wide, dark brown, gynophore 4–6 cm long, glabrate; seeds suborbicular, ca. 1.5 cm long, 1.0–1.5 cm wide, surface dull, dark brown, funicular aril-lobe scars extending ½ way around edge of seed.

Bauhinia multinervia occurs in our range only in the Lesser Antilles where it is found in mesic forests at elevations up to about 900 m. This species also occurs in Venezuela, Suriname, and Brazil. It is sometimes cultivated as a novelty within its natural range and in tropical areas outside it. *Bauhinia multinervia* flowers throughout the year, but most abundantly from October to March. This species is pollinated by bats.

Bauhinia multinervia is distinguished from other Bauhinias in our range by its large flowers. It is a part of the *B. ungulata* complex, which consists of about 50 species centered in the Planalto region of Brazil.

None of the collections of *B. multinervia* seen from the Lesser Antilles have been made since the late 1930's.

In Venezuela the species is known by the local names "Guarapo" and "Uripe."

Specimens examined: ANTIGUA. Northwest (volcanic district), Fig Tree Hill, *Box 1259* (UC, US); without precise locality, *Rose et al. 3401* (US). GUADELOUPE. Without precise locality, *Beaupertuis s.n.* (P); *Questel 690* (US); *Richard s.n.* (P). MARTINIQUE. St. Lucie. *Stehlé & Stehlé 3550* (US); without precise locality. *Belanger 490* (P); *Duss 1124* (NY); *Terrasson 44* (P). ST. VINCENT. Without precise locality, *Smith & Smith 273* (NY).

17. Bauhinia pansamalana Donn. Sm., Bot. Gaz. 13: 27. 1888. *Casparia pansamalana* (Donn. Sm.) Britt. & Rose, N. Amer. Fl. 23: 216. 1930. TYPE: Guatemala. Alta Verapaz: Pansamala, *Tuerckheim 681* (holotype, US; isotypes, NY, P).

Shrubs or small trees up to 5 m tall; branches glabrous. Leaves chartaceous, ovate, entire or bilobed up to ⅓ their length, lobes slightly divergent, 12–22 cm long, 9–15 cm wide, base cordate to rounded, apex of entire leaf acuminate to caudate, apex of lobes acuminate, margins smooth or nearly so, glabrous on both surfaces, 7-nerved; petiole 3–6 cm long, slightly canaliculate, glabrous; stipules not seen, caducous; intrastipular excrescences minute. Inflorescences paniculate, terminal, or subterminal and axillary, 20–40-flowered, rachis and rachilla strigose to glabrate, buds linear, ca. 2 cm long, strigose, free tips minute; bract ovate, ca. 1 mm long; bracteoles similar to bract; pedicels ca. 1.5 cm long, strigose; hypanthium cyathiform, 4–6 mm long; calyx spathaceous at anthesis; petals 5, subequal, white, 2.0–2.5 cm long, blade narrowly elliptic, ca. 2 times the length of the sparsely pilose claw, 2–3 mm wide, glabrate; fertile stamens 3, subequal, adnate with staminodes, subequalling petals, adaxillary and each separated by staminode, filaments slender, arcuate, pilose at base, anthers 4–5 mm long, glabrous, stamens and staminodes sparsely pilose on inner surface; staminodes

subequal, 7–9 mm long, connate for ½ or more their length, abortive anthers present or absent; pollen spheroid, inaperturate, sexine reticulate with blunt, spinelike infratectal processes; gynoecium subequalling petals, arcuate, ovary strigose, gynophore and style glabrate, gynophore subequalling style, stigma oblique, slightly differentiated from style. Fruit linear, apiculate with persistent style, 20–30 cm long, 2.0–2.5 cm wide, glabrous, gynophore 4–6 cm long, glabrate; seeds not seen.

Bauhinia pansamalana is a rare species native to southern Mexico and Guatemala. It occurs in moist deciduous or tropical rainforests up to 1,200 meters in elevation. It flowers from April to July.

Bauhinia pansamalana is the only Middle American species of *Bauhinia,* other than *B. coulteri,* that has three fertile stamens. It occurs well to the south of the range of *B. coulteri* and can be further distinguished from that species by its large leaves.

Specimens examined: MEXICO. CHIAPAS: Finca Irlanda, *Purpus 7302* (F, GH, MO, NY, UC, US). VERACRUZ: Rio Soloxoxhil between Cedillo and La Escuadra, *Vázquez et al. V-338* (MEXU). GUATEMALA. ALTA VERAPAZ: Between Sepacuite and Secoyocte, *Pittier 333* (F, MO, NY, US); near Chirriacte on Petén Highway, *Standley 91659* (F, US); *Standley 91858* (F); Pansamala, *Donnell Smith 1631* (US); near Finca Sepacuiter, *Cook & Griggs 581* (US). IZABAL: Along Río Bonita, *Steyermark 41738* (F).

18. Bauhinia pauletia Pers., Syn. Pl. 1: 455. 1805. Based on *Pauletia aculeata* Cav.

Pauletia aculeata Cav., Icon. 5: 6. 1799. TYPE: Panama. Panama: ?Near Panama City, *Herb. Cavanilles* (holotype, MA, not seen).
Bauhinia spinosa Poir., Encyc., Suppl. 1: 599. 1811. Based on *Pauletia aculeata* Cav.
Bauhinia panamensis Spreng., Syst. Veg. 2: 334. 1825. Based on *Pauletia aculeata* Cav.
Bauhinia leptopetala DC., Prodr. 2: 513. 1825. TYPE: Based on a Sessé and Mociño Plate (copy, G, not seen; photograph of copy at G, F, MO, US; tracing of copy at G, US; photograph of tracing of copy at G, MO, US; blueprint of tracing of copy at G, MO, US).
Bauhinia parvifolia Seem., Bot. Voy. Herald 113. 1854; non Hochst. ex Field. & Gard., 1844; non Teijsm. & Binn., 1867. TYPE: Panama. Panamá: Panamá Viejo, *Seemann 223* (holotype, K; photograph of holotype, F, NY, US).
Bauhinia chlorantha Brandeg., Zoë 5: 200. 1905. TYPE: Mexico. Sinaloa: Vicinity of Culiacán, *Brandegee s.n.* (holotype, UC; isotype, US).
Bauhinia longiflora Rose, Contr. U.S. Nat. Herb. 10: 97. 1906; non (Bong.) Steud., 1840. TYPE: Mexico. Sinaloa: Ymala, *Palmer 1426* (holotype, US; isotypes, F, NY, UC, US).

Shrub or small tree up to 5(–8) m tall; branches often subscandent, strigose or sparsely pilose when young, soon glabrate, armed with 1–2 intrastipular spines up to 6 mm long. Leaves chartaceous, broadly ovate to suborbicular, bilobate for ¼, rarely ½ their length, lobes divergent, (3–)4–6(–7) cm long, (3–)4–6(–7) cm wide, base cordate to rounded, apex of lobes rounded to obtuse, margins smooth or nearly so, upper surface glabrous, lower surface strigose and often sparsely pilose, pilose on nerves below, (7–)9-nerved; petiole 1–3 cm long, slightly canaliculate, pilose or strigose, rarely glabrate; stipules filiform, ca. 5 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a broad-based, occasionally reflexed spine, others minute. Inflorescence 1–2-flowered, axillary, subterminal, appearing racemose through suppression of subterminal leaves, buds filiform, bases inflated, 8–10(–12) cm long, strigose, free tips setaceous, 5–10 mm long; bract broadly to narrowly lanceolate, 2–4 mm long; bracteoles similar to bract; peduncle up to 3 mm long, pedicels 0.5–1.5 cm long, strigose or pilose; hypanthium suburceolate, 1–2 cm long, pilose on inner surface; calyx spathaceous or splitting into 2–5 lobes at anthesis, limb(s) twisting; petals 5, subequal, filiform, greenish-white, 4–6 cm long, 0.5–1.0 mm wide, glabrous, coiling and reflexed at anthesis; fertile stamens 5, 10–12 cm long, filaments filiform, spreading, glabrous, basally adnate with staminodes, anthers linear, 2.5–3.0 cm long, apex apiculate, base sagittate; staminodes 5, subequal, filiform, 3–5 cm long, glabrous, abortive anthers absent; pollen spheroid, 4–6-colpate, sexine reticulate with clavate supratectal processes; gynoecium subequalling stamens, slightly arcuate, ovary tomentose, gynophore and style glabrate, gynophore subequalling style, stigma lanceolate with lateral receptive surface. Fruit linear, apiculate with persistent style, (15–)20–25(–30) cm long, ca. 1.5 cm wide, light brown or tan, velutinous to glabrate at maturity, gynophore 4–6 cm long, glabrate; seeds oblong to suborbicular, 6–8 mm long, 5–7 mm wide, surface dull, chestnut-brown, funicular aril-lobe scars equal, 3–4 mm long.

Bauhinia pauletia ranges from western Mexico south to Colombia and Venezuela. In has been introduced into Puerto Rico where it has become

naturalized. It occurs in dry deciduous thorn forests and disturbed areas at elevations up to 400 m. It flowers throughout the year but most abundantly from May to January. It is known to be pollinated by at least two species of bats and has a high degree of andromonoecism (Heithaus et al., 1974).

Bauhinia pauletia is one of only two spiny species of *Bauhinia* within the range of this study. It is readily distinguished from the other species, *B. aculeata,* by its filiform buds 8–12 cm long, greenish-white, filiform petals, and five fertile stamens. It is closely related to a group of about six species in South America.

In Colombia the species is known by the local names "Pata de Vaca" and "Guajaro," in El Salvador as "Pie de Cabra," "Pie de Venado," and "Garrabatillo," in Guatemala as "Uña de Gato," in Honduras as "Garrabatillo," in Mexico as "Uña de Gato" and "Pie de Cabra," and in Panama as "Cuchillito."

Representative specimens: MEXICO. CHIAPAS: Above Finca Carmen, along road from Acalá to Pugiltik, *Ton 3057* (DUKE, NY). COLIMA: Ca. 15 mi. SE of Manzanillo, *McVaugh & Koelz 1618* (MICH). GUERRERO: Balsas Station, *Pringle 10112* (CM, MO, MSC, NY, UC, US, VT). JALISCO: Ca. 2 km N of Puerto Vallarta W of airport, *Feddema et al. 2559* (DUKE, MICH, TEX, US, WIS). MÉXICO: Naranjo, *Hinton 1990* (NY, US). MICHOACÁN: 4 mi. NW of Apatzingán, *McVaugh 17893* (DUKE, LL, MICH, US). MORELOS: *Sine loc.*, *Lemmon & Lemmon 266* (UC). NAYARIT: 14 mi. SE of Saylita, *Johnson 297-73* (UNAF). OAXACA: Tapanatepec, along Mexican Highway 190, *Breedlove & Raven 13678* (F, LL, MICH, US). SINALOA: Culiacán, *Gentry 5027* (F, MICH, MO, NY, UC, US). VERACRUZ: Juan Covarrubias, *Calderón 2008* (F, MEXU). GUATEMALA. JUTIAPA: Laguna de Guija, *Heyde & Lux 6324* (NY, US). SANTA ROSA: Llano Entero, SE of Chiquimulilla, *Standley 78837* (F). HONDURAS: CHOLUTECA: Near Choluteca, *Williams & Molina 10857* (F). COPÁN: Along Río Copán, 3 km from Santa Rita on way to La Entrada, *Molina & Molina 24711* (MO, NY). OCOTEPEQUE: Along Río Lempa, road to Esquipulas, *Molina 22404* (F). VALLE: Near Amapala, Isla Tigre, *Standley 20711* (US). EL SALVADOR. LA PAZ: Km 37 toward Zacatecoluca, *Fassett 29176* (MICH). LA UNIÓN: Vicinity of La Unión, *Standley 20694* (NY, US). SAN MIGUEL: Ca. 15 km NE of San Miguel, *Tucker 469* (F, MICH, UC, US). SANTA ANA: Vicinity of Metapán, *Standley & Padilla 3281* (F, UC). SAN VICENTE: 3 mi. W of Río Lempa near San Nicolás Lempa, *Wunderlin 5031* (MO). USULUTAN: Hacienda Concordia, *Calderón 2093* (US). NICARAGUA. GRANADA: Near Granada, *Maxon et al. 7623* (US). LEÓN: Quesalguaque, *Baker 89* (MICH, MO, NY, UC). MANAGUA: S of Managua, *Garnier 219* (US). MASAYA: Parque Nacional Volcán Masaya, *Neill 2803* (MO, USF). COSTA RICA. GUANACASTE: Bebebero Road, 1.3 km W of Canas, *Heithaus 390* (MO). PANAMA. CANAL ZONE: Between Miraflores and Corozal, *Pittier 2202* (F, NY, US). COCLÉ: Road to Contractor's Hill, *Dwyer 7224* (MO). HERRERA: Vicinity of Chitre, *Allen 1086* (MO, US). LOS SANTOS: 6 mi. S of Las Tablas, *Croat 9719* (DUKE, MO, SCZ). PANAMÁ: Las Sabanas, *Standley 25841* (MO, US). PUERTO RICO. MAYAGUEZ: Between La Plata and Sabana Grande, *Urban 3852* (MO, MSC, NY, US).

19. Bauhinia pes-caprae Cav., Icon. 5: 3. 1799. *Casparia pes-caprae* (Cav.) H.B.K., Nov. Gen. Sp. Pl. 6: 318. 1824. *Mandarus pes-caprae* (Cav.) Raf., Sylva Tellur. 122. 1838. TYPE: Mexico. Guerrero: *Nee s.n.* (holotype, MA, not seen; fragment of holotype, F; photograph of holotype, F, MO, US).

Bauhinia aegopoda St.-Lag., Ann. Soc. Bot. Lyon 7: 69. 1880, nom. illeg. (New name for *Bauhinia pes-caprae* Cav.)

Shrub or small tree up to 4(–6) m tall; branches strigose when young, soon glabrate. Leaves coriaceous, ovate to oblong, bilobate for ¾ or more their length, lobes parallel or rarely slightly divergent, (2–)4–6(–9) cm long, (2.5–)4–6(–8.0) cm wide, base deeply cordate, apex of lobes rounded to obtuse, margins slightly to moderately crisped, upper surface glabrous, lower surface strigose to glabrate, (5–)7-nerved; petiole 1–2 cm long, slightly canaliculate, strigose or glabrous; stipules ovate, apiculate, ca. 1 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 1.5 mm long, others minute. Inflorescences racemose, terminal, frequently with additional subterminal axillary racemes, 30–60-flowered, rachis strigose, buds narrowly elliptic, 1.3–1.8 cm long, reflexed when young, erect at anthesis, densely strigose with white or tan hairs, free tips minute; bract ovate to lanceolate, 1.0–1.5 mm long; bracteoles similar to bract but smaller; pedicel slender, 1.5–2.0 cm long, strigose; hypanthium cyathiform, 1–2 mm long; calyx spathaceous at anthesis; petals 5, subequal, white, (1.5–)2.0–2.5(–3.0) cm long, blade narrowly elliptic, ¼ or less than the length of claw, 1–2 mm wide, pilose, claw densely pilose; fertile stamen 1, subequalling petals, filament slender, slightly arcuate, pilose at base, connate with staminodes, anther linear, 4–5 mm long, strigose; staminodes 9, subequal, 7–10 mm long, connate for ⅓ or less their length, densely pilose except for short tips, abortive anthers absent or rarely present; pollen spheroid, 3-colporoidate, sexine reticulate; gynophore equalling or slightly exceeding petals, slightly arcuate, stri-

gose, gynophore subequalling style, stigma small, capitate. Fruit linear, apiculate with persistent style, (5–)8–10(–12) cm long, 1.5–2.0 cm wide, light brown, glabrate, gynophore ca. 2 cm long, strigose; seeds oblong, 7–9 mm long, 4–7 mm wide, surface dull, dark brown, funicular aril-lobe scars subequal, ca. 2 mm long.

Bauhinia pes-caprae is known only from along the southwestern coast of Mexico in the states of Guererro and Oaxaca. Most collections are from within a few miles of Acapulco. It occurs in dry, rocky, calcareous soils in open deciduous woods at elevations from near sea level up to 100 m. It flowers from January to April.

This species is most closely related to *B. pringlei* and *B. subrotundifolia,* from which it is distinguished by reflexed buds and deeply bilobate coriaceous leaves with nearly parallel lobes.

The local name is "Pie de Cabra."

Representative specimens: MEXICO. GUERERRO: Acapulco and vicinity, *Palmer 441* (A, F, GH, MICH, MO, NY, UC, US). OAXACA: W of Tehuantepec at Km 79 on road to Oaxaca, *Barr & Mason 2373* (UC).

20. **Bauhinia petiolata** (Mutis ex DC.) Triana ex Hook. f., Bot. Mag. t. 6277. 1877. *Amaria petiolata* Mutis ex DC., Prodr. 2: 519. 1825. TYPE: Colombia. *Mutis 2398* (holotype, MA, not seen; isotype, US).

Amaria sessilifolia Mutis ex DC., Prodr. 2: 519. 1825. TYPE: Colombia: *Mutis 2724* (holotype, MA, not seen; fragment of holotype, US).

Casparia speciosa Linden ex Hook. f., Bot. Mag. t. 6277. 1877, pro syn.

Bauhinia caudigera Blake, Contr. U.S. Nat. Herb. 20: 533. 1924. *Schnella caudigera* (Blake) Pittier, Suppl. Pl. Usual. Venez. 37. 1939. TYPE: Venezuela. Carabobo: Guaremales, road from Puerto Cabello to San Felipe, *Pittier 8851* (holotype, US; isotype, P; photograph of holotype, NY, US).

Shrubs or small trees to 8 m tall; branches slender, glabrous. Leaves chartaceous, ovate to ovate-lanceolate, entire, 7–14 cm long, 3–7 cm wide, base rounded to truncate, apex caudate, upper surface glabrous, lower surface obscurely strigillose along the veins or glabrate, 5-nerved; petiole 1–3 cm long, slightly canaliculate; stipules ovate to réniform, ca. 1 mm long, persistent and becoming calloused, intrastipular excrescences obscure. Inflorescences short-racemose, terminal, or subterminal and axillary, the racemes 3–8-flowered, the rachis tomentellous or glabrate, buds narrowly ellipsoid, ca. 4 cm long, tomentellous to glabrate; bract broadly ovate, ca. 1 mm long, ciliolate; bracteoles similar to bract; pedicels 4–7 mm long; hypanthium campanulate, 5–10 mm long; calyx spathaceous at anthesis; petals 5, subequal, 3–5 cm long, white, blade oblanceolate, 1.0–1.5 cm wide, glabrous, claw 2–5 mm long, glabrous; fertile stamens 10, slightly shorter than petals, the alternate ones slightly shorter, slightly connate at base, glabrate, anthers linear, 7–10 mm long, sparsely pilose or glabrate; pollen spheroid, inaperturate, sexine reticulate with blunt, spinelike infratectal processes; gynoecium 4–5 cm long, subequalling androecium, glabrous, ovary 2–3 cm long, style ca. 1.5 cm long, arcuate, stigma oblique, bilobate, gynophore subequalling the style or slightly shorter, stigma bilobate. Fruits linear, apiculate with persistent style, 20–30 cm long, 2–3 cm wide, glabrous, the gynophore ca. 2 cm long; mature seeds not seen.

Bauhinia petiolata is an uncommon species known from a few scattered localities in Colombia and Venezuela, and from a single collection in Panama. It occurs in tropical wet forests from near sea level up to 600 m. It has been collected in flower from February to July.

Bauhinia petiolata resembles *Bauhinia beguinotii* but differs in smaller leaves, stamens free to the base, and the main leaf nerves equidistant or closer to adjacent nerves than to the midrib. It also resembles *B. jenningsii,* but differs in stamen number.

Specimen examined: PANAMA. COLÓN: Ca. 2–3 mi. up the Río Guanche, *Kennedy & Foster 2127* (MO, USF).

21. **Bauhinia picta** (H.B.K.) DC., Prodr. 2: 515. 1825. *Pauletia picta* H.B.K., Nov. Gen. Sp. Pl. 6: 316. 1824. TYPE: Colombia. Santander: Along the Río Magdalena near the confluence with Río Opon, between Bohorquez and Isla de Brujas, *Humboldt 1604* (holotype, P; isotype, B(W), not seen; photograph of B isotype, F, MO, NY, US).

Bauhinia ligulata Pittier, Contr. U.S. Nat. Herb. 20: 112. 1918. TYPE: Panama. San Blas: Near Puerto Obaldia, *Pittier 4334* (holotype, US; fragment of holotype, NY; isotypes, F, NY, US).

Bauhinia kalbreyeri Harms, Repert. Spec. Nov. Regni Veg. 19: 65. 1923. TYPE: Colombia. Antioquia: Murri, *Kalbreyer 1802* (holotype, B, destroyed in World War II; fragment of holotype, F; photograph of holotype, F, MO, NY, US; isotypes, K, US; photograph of K isotype, F, NY, US).

Bauhinia conceptionis Britt. & Killip, Ann. New York

Acad. Sci. 35: 160. 1936. TYPE: Colombia. Chocó: La Concepción, 15 km E of Qyibdó, *Archer 2086* (holotype, NY; isotype, US).

Large trees up to 40 m tall; branches ferruginous tomentose when young, soon glabrate. Leaves chartaceous, ovate, bilobate for ca. ¼ or less their length, lobes slightly divergent, 4–10 cm long, 4.0–7.5 cm wide, base cordate to rounded, apex of lobes caudate to obtuse, upper surface glabrous, lower surface ferruginous tomentellous, at least on nerves, or glabrate, 9–13-nerved, petioles 2–3 cm long, slightly canaliculate, ferruginous tomentellous to glabrate; stipules ovate, ca. 1 mm long, scarious, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 2 mm long, others minute. Inflorescences short-racemose, axillary, subterminal, 10–20-flowered, flowers solitary or geminate, rachis ferruginous tomentose, buds elongate-clavate, 2.0–2.5 cm long, ferruginous tomentose, free tips minute; bract lanceolate, ca. 1 mm long; bracteoles similar to bract; pedicels 2–6 mm long, ferruginous tomentose; hypanthium campanulate, 6–8 mm long; calyx spathaceous, lobes sometimes becoming partly free; petals 5, subequal, white or pinkish with roseate center, 2–3 cm long, blade ovate-elliptic, 6–13 mm wide, glabrous, claw 2–4 cm long, glabrous or with a few short trichomes; fertile stamens 10, 5 subequalling petals, alternate ones slightly shorter, free to base or shortly connate, staminal sheath ligulate, tomentose on inner surface; pollen spheroid, inaperturate, sexine reticulate with blunt, spinelike infratectal processes; gynoecium subequalling stamens, ovary tomentose, style tomentellous, subequalling gynophore, stigma capitate, gynophore tomentellous. Fruit linear, apiculate with persistent style, 15–25 cm long, ca. 2.0 cm wide, gynophore 1–2 cm long, glabrate; seeds not seen.

Bauhinia picta is native to Colombia, Venezuela, and Panama. It occurs in light to heavy forests at elevations from near sea level up to about 1,500 m. In our range it is known only from the type collection of *Bauhinia ligulata* Pittier in Panama.

It is distinguished from other members of the Petiolata alliance by its usually pinkish flowers and ligulate staminal sheath.

In Colombia the local names are "Pata de Vaca," "Pate-buey de Monte," "Algodoncillo," "Casco de Vaca," and "Pate Buey."

22. **Bauhinia pringlei** S. Wats., Proc. Amer. Acad. Arts 25: 147. 1890. *Casparia pringlei* (S. Wats.) Britt. & Rose, N. Amer. Fl. 23: 212. 1930. TYPE: Mexico. Jalisco: Near Guadalajara, *Pringle 1722* (holotype, US; isotypes, A, F, GH, NY, P, UC, US, VT).

Shrub or small tree up to 5(–40) m tall; branches strigulose when young, soon glabrate. Leaves chartaceous, broadly ovate to suborbicular, bilobate for ½ to ¾ their length, lobes slightly divergent, (5–)8–16(–18) cm long, (5–)7–15(–17) cm wide, base cordate to rarely truncate, apex of lobes rounded to obtuse, margins slightly to moderately crisped, upper surface glabrous, lower surface strigose to glabrate, 7–9(–11)-nerved; petiole 3–5(–7) cm long, slightly canaliculate, strigose to glabrate; stipules ovate, apiculate, ca. 1 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 1.5 mm long, others minute. Inflorescence racemose, terminal, frequently with additional subterminal axillary racemes, 20–40-flowered, rachis strigose, buds linear-lanceolate, 1.5–2.0 cm long, densely strigose with white hairs, free tips minute; bract ovate to lanceolate, 1.0–1.5 mm long; bracteoles similar to bract but smaller; pedicels slender, 1.5–2.2 cm long, strigose; hypanthium cyathiform, 1–2 mm long; calyx spathaceous at anthesis; petals 5, subequal, white with a red median stripe, (1.5–)2–3(–3.5) cm long, blade narrowly elliptic, ca. twice the length of claw, 4–5 mm wide, glabrous or pilose at base, claw pilose; fertile stamen 1, ½ to ¾ as long as petals, filament slender, pilose at base, connate with staminodes, anther linear, 4–6 mm long, glabrate; staminodes 9, subequal, 5–7 mm long, connate for ⅓ or less their length, pilose ca. ½ their length, tips purplish, abortive anthers usually present, rarely absent; pollen spheroid, 3-colporoidate, sexine striato-reticulate; gynoecium subequalling petals, slightly arcuate, ovary strigose, style strigose, stigma small, capitate, gynophore subequalling the style, pilose toward base or glabrous. Fruit linear, apiculate with persistent style, (8–)10–12(–15) cm long, 1–2 cm wide, light brown, glabrous, gynophore ca. 2 cm long, glabrous; seeds suborbicular, 8–10 mm long, 6–9 mm wide, surface more or less shining, chestnut-brown, funicular aril-lobe scars unequal, one 2 mm, other 3.5 mm long.

Bauhinia pringlei occurs only in western Mexico on dry calcareous soils in open deciduous

forests at elevations from near sea level up to 800 meters. It flowers from November to January.

It is distinguished from all other monandrous species of *Bauhinia* by its white petals with a distinct median stripe. It is most closely related to *B. subrotundifolia* and *B. pes-caprae.*

The local name is "Pata de Venado."

Representative specimens: MEXICO. GUERRERO: N of Río Balsas, Achotla, Barranca de la Juntas, *Mexia 8899* (F, GH, LL, MO, NY, UC, US). JALISCO: Barranca de Guadalajara, *Pringle 9723* (CM, F, GH, MO, NY, US, VT). MÉXICO: Guayabal, *Hinton 5384* (A, MO, US). SINALOA: Cuesta de Tatamoza, road to Comedero, *Gentry 5378* (GH, MEXU, MICH, MO, NY). ZACATECAS: 2 mi. N of Santa Rosa on Highway 41, ca. 42 mi. SW of Jalpa, *Mahler & Thieret 5842* (NY).

23. **Bauhinia ramosissima** Benth. ex Hemsl., Diag. Pl. Nov. 49. 1880. *Casparia ramosissima* (Benth. ex Hemsl.) Britt. & Rose, N. Amer. Fl. 23: 210. 1930. TYPE: Mexico. Hidalgo: Zimapán, *Coulter 473* (holotype, K; photograph of holotype, NY, US).

Bauhinia unguicularis Benth. ex Hemsl., Diag. Pl. Nov. 49. 1880. *Casparia unguicularis* (Benth. ex Hemsl.) Britt. & Rose, N. Amer. Fl. 23: 210. 1930. TYPE: Mexico. Hidalgo: Zimapán, *Coulter 472* (holotype, K; photograph of holotype, A, F, NY, US).

Bauhinia uniflora S. Wats., Proc. Amer. Acad. Arts 21: 451. 1886; non Hassler, 1911. *Casparia uniflora* (S. Wats.) Britt. & Rose, N. Amer. Fl. 23: 209. 1930. (TYPE: Mexico. Coahuila: Jimulco, *Pringle 174* (holotype, US; isotypes, CM, F, NY, P, US, VT).

Casparia monantha Britt. & Rose, N. Amer. Fl. 23: 209. 1930. *Bauhinia monantha* (Britt. & Rose) Lundell, Phytologia 1: 214. 1937. TYPE: Mexico. Coahuila: General Cepeda, *Palmer 330* (holotype, US; isotypes, CM, F, MO, NY, UC).

Casparia purpusii Britt. in Britt. & Rose, N. Amer. Fl. 23: 210. 1930. *Bauhinia purpusii* (Britt.) Lundell, Phytologia 1: 214. 1937. TYPE: Mexico. Hidalgo: Ixmiquilpan, *Purpus 1364* (holotype, NY; isotypes, F, MO, UC).

Casparia runyonii Britt. & Rose, N. Amer. Fl. 23: 210. 1930. *Bauhinia runyonii* (Britt. & Rose) Standl., Trop. Woods 34: 41. 1933. TYPE: Mexico. Tamaulipas: Mountains near Ciudad Victoria, in canyon on road to Jaumave, *Runyon 748* (lectotype, US; isolectotype, NY). Lectotype here designated.

Densely branched shrub up to 3 m tall; branches strigose when young, soon glabrate. Leaves subcoriaceous, bifoliolate, leaflets oblong to suborbicular, inner margins more or less parallel, (0.5–)1.5–2.5(–3.0) cm long, (0.5–)1.0–1.5(–2.0) cm wide, base cuneate, apex rounded, margins slightly crisped, upper surface glabrous, lower surface strigose to glabrate, 2(–3)-nerved; petiole 3–10 mm long, slightly canaliculate, strigose; stipules ovate to lanceolate, ca. 1.5 mm long, caducous; intrastipular excrescences minute. Inflorescences short-racemose or flowers solitary, terminal, or subterminal and axillary, 1–6-flowered, rachis strigose, buds narrowly lanceolate, 1.5–2.0 cm long, usually purple, tip often prolonged up to 5 mm, free tips up to 1.5 mm long; bract lanceolate, 1.0–1.5 mm long; bracteoles similar to bract, but smaller; pedicels 3–6 mm long, strigose; hypanthium cyathiform, 1–2 mm long; calyx spathaceous at anthesis; petals 5, subequal, purple, (1.5–)2.0–2.5(–3.0) cm long, blades elliptic, ca. ⅓ the length of claw, 3–8 mm wide, glabrous or sparsely pilose at base, claw tomentose; fertile stamen 1, shorter than or equalling petals, filament slender, arcuate, glabrous or sparsely pilose near base, short-connate with staminodes, anther oblong, 7–9 mm long, glabrate; staminodes 9, subequal, 2–5(–7) mm long, connate for ca. ½ their length, tomentose on inner surface, usually tomentose on outer surface near base, tip glabrous, purplish-tinged, abortive anthers present or absent; pollen spheroid, 3-colporoidate, sexine striato-reticulate; gynoecium subequalling petals, arcuate, pilose, gynophore subequalling style, stigma small, capitate, slightly differentiated from style. Fruit linear, apiculate with persistent style, (5–)6–8(–9) cm long, 0.5–1.5 cm wide, light brown, strigose or glabrate, gynophore ca. 1 cm long, glabrate; seeds oblong to suborbicular, 5–8 mm long, 4–8 mm wide, chestnut-brown, surface dull, funicular aril-lobe scars equal, ca. 2.5 mm long.

Bauhinia ramosissima occurs in northeastern and central Mexico on rocky, calcareous soil in desert shrub communities at elevations of 800 to 2,500 m. It flowers throughout the year depending on sufficient moisture.

This species is distinguished from all other *Bauhinia* species within its range in that it is the only one that is both purple-flowered and bifoliolate. The only other bifoliolate species within its range, *B. lunarioides*, has white flowers. *Bauhinia ramosissima* is most closely related to *B. macranthera* with which it is sometimes confused. *Bauhinia macranthera* normally has bilobate but may rarely have bifoliolate leaves. However, *B. ramosissima* may be distinguished from *B. macranthera* by smaller, fewer-nerved

leaves and smaller flowers without conspicuous setaceous tips on the calyx.

Britton and Rose (1930) recognized six species that are here reduced to one. They were distinguished by leaf shape, number of flowers in the inflorescence, and petiole length; characters all too variable to be of value. There is a large amount of variation within both *B. ramosissima* and *B. macranthera.* Additional field study may show that some populations represent distinct taxa. On the basis of the data at hand at this time it seems best to recognize only two, distinct but variable species.

Britton and Rose's *Casparia runyonii* posed a problem because the paratypes belong to two different species. The specimens collected April 8, 1926, are *B. ramosissima* while those collected March 27, 1925, are *B. macranthera.* The protolog of the species is inadequate to determine with certainty which species Britton and Rose intended. It is perhaps a composite of the two species. The specimens also give no clue to resolve the matter. In their key, the species is placed close to *B. unguicularis* (which is now placed in synonymy with *B. ramosissima*) and I have elected to lectotypify the name in the sense of *B. ramosissima.*

Representative specimens: MEXICO. CHIHUAHUA: Near Cañón del Rayo, NE side of N end of Sierra del Diablo, *Stewart 936* (GH, TEX). COAHUILA: Sierra de la Paila, *Purpus 4742* (F, MO, UC, US). DURANGO: Sierra de Banderas, 54 km N of Bermejillo, *Chiang et al. 8302.* HIDALGO: Near Ixmiquilpan, *Rose et al. 9037* (US). NUEVO LEÓN: 14 km N of Matehuala, *Ripley & Barneby 13293* (NY). SAN LUIS POTOSÍ: Minas de San Rafael, Sierra de Guascama, *Purpus 5186* (F, MEXU, MO, NY, UC, US). TAMAULIPAS: Near Miquihuana, *Stanford et al. 783* (GH, MO, NY, UC). ZACATECAS: 2 km E of El Farolito, off Caopas-Tecolotes highway, *Johnston et al. 10464* (TEX).

24. **Bauhinia rubeleruziana** Donn. Sm., Bot. Gaz. 13: 27. 1888. *Casparia rubeleruziana* (Donn. Sm.) Britt. & Rose, N. Amer. Fl. 23: 214. 1930. TYPE: Guatemala. Alta Verapaz: Rubeleruz, *Tuerckheim 896* (holotype, US; isotypes, NY, P, US).

Bauhinia emarginella Standl., Publ. Carnegie Inst. Wash. no. 461. 60. 1935. TYPE: Belize. Toledo: Camp 32, British-Guatemala boundary, *Schipp S630* (holotype, F; isotypes, MO, NY).

Bauhinia palenquensis Lundell, Contr. Univ. Mich. Herb. 6: 24. 1941. TYPE: Mexico. Chiapas: Palenque, *Matuda 3666* (holotype, MICH; isotypes, F, NY).

Tree up to 15(–25) m tall; branches tomentose with yellowish-brown hairs when young, glabrate in age. Leaves chartaceous, ovate to oblong ovate, bilobate for ⅓ or less their length, emarginate or entire, 8–15 cm long, 5–12 cm wide, base cordate to rounded, apex of lobes acute to rounded, apex of entire leaves rounded to apiculate, margins smooth to slightly crisped, upper surface occasionally tomentellous on midvein, otherwise glabrous, lower surface tomentose to tomentellous with yellowish-brown hairs, 7–9-nerved; petiole 1.5–3.0 cm long, slightly canaliculate, tomentose with yellowish-brown hairs; stipules linear, ca. 1.5 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection ca. 1.5 mm long, others minute. Inflorescences racemose, subterminal, axillary, racemes usually 20–30-flowered, rachis tomentose with yellowish-brown hairs, buds linear-lanceolate, 1.5–2.0 mm long, frequently reddish-tinged, reflexed when young, ascending at anthesis, tomentose to tomentellous, free tips ca. 1 mm long; bract linear, ca. 4 mm long; bracteoles linear, ca. 2 mm long; pedicels 1–2(–2.5) cm long, tomentose with yellowish-brown hairs; hypanthium cyathiform, 2–3 mm long; calyx spathaceous at anthesis, reddish on inner surface; petals 5, subequal, brick-red, 1.5–2.5 cm long, blade narrowly elliptic, ca. 2 times as long as claw, 1.5–4.0 mm wide, sparsely pilose near tip on inner surface, claw glabrate; fertile stamen 1, subequalling petals, filament slender, arcuate, glabrous, connate with staminodes, anther linear-oblong, 3–4 mm long, glabrous; staminodes 9, subequal, 10–15 mm long, connate for ⅓ or less their length, glabrous on outer surface, pilose on inner surface near and below connate part, abortive anthers present or absent; pollen spheroid, 3-colporoidate, sexine striate; gynoecium equalling or exceeding stamen, arcuate, ovary short pilose to tomentose, gynophore and style with fewer hairs, gynophore subequalling style, stigma small, not much differentiated from style. Legume linear, apiculate with persistent style, 10–16 cm long, ca. 2 cm wide, brown, glabrate, gynophore ca. 1.5 cm long, glabrate; seeds oblong to suborbicular, 9–12 mm long, 7–9 mm wide, surface dull, brown, funicular aril-lobe scars subequal, ca. 3 mm long.

Bauhinia rubeleruziana is an uncommon species occurring in moist deciduous forests and rainforests of southern Mexico, Guatemala, and Belize at elevations of 100 to 800 m. It flowers from March to July.

Bauhinia rubeleruziana is distinguished from all other species of *Bauhinia* within its range by its brick-red flowers in dense clusters. It is most

closely related to *B. divaricata* but distinguished from that species by yellowish-brown hairs on the lower surface of young leaves and branches.

Representative specimens: MEXICO. CHIAPAS: Between the Río Chocoljanto and the Río Chancala, E of Santa Margarita, *Gómez-Pompa 343* (US). GUATEMALA. ALTA VERAPAZ: Cubilquitz, *Tuerckheim 7841* (MO, NY, US, VT). PETÉN: 3 km S of Poptun, *Harmon 2508* (LL, MO, UMO). BELIZE. CAYO: Retiro Spring Camp Road, *Lamb 79* (F).

25. **Bauhinia seleriana** Harms in Loess., Bull. Herb. Boissier 7: 549. 1899. TYPE: Guatemala. Huehuetenango: Near Quen Santo, *Seler & Seler 2797* (holotype, B, destroyed in World War II; fragment of holotype, F; photograph of holotype, F, MO, NY, US; isotypes, K, NY, US; photograph of K isotype, F, NY, US).

Bauhinia paradisi Standl. & L. O. Williams, Ceiba 1: 80. 1950. TYPE: Honduras. El Paraíso: Río Lizapa floresta de robles area, between Galeras and Lizapa Grande, *Molina 860* (holotype, US; photograph of holotype, NY; isotype, F).

Shrub or small tree up to 12 m tall; branches short-hirsute when young, soon glabrate. Leaves chartaceous, broadly ovate, bilobate for ca. ⅓ their length, lobes slightly divergent, 6–10 cm long, 6–10 cm wide, base cordate to rounded, apex of lobes obtuse to rounded, upper surface glabrous, lower surface short hirsute or tomentellous, 9–11-nerved; petioles (1–)2–4(–5) cm long, slightly canaliculate, hirsute or tomentellous; stipules ca. 4 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 1.5 mm long, others minute. Inflorescences racemose, terminal, or subterminal and axillary, 5–30-flowered, rachis short-hirsute or tomentellous, buds elliptic, 8–15 mm long, short-hirsute or tomentellous, free tips up to 2 mm long; bract lanceolate to linear, 1–4 mm long; bracteoles similar but slightly smaller than bract; pedicels 4–5 mm long, hirsute or tomentellous; hypanthium cyathiform, 1–2 mm long; calyx spathaceous at anthesis; petals 5, subequal, white, 11–18 mm long, blade elliptic, 4–8 mm wide, apiculate, pilose on tip, claw ca. 1 mm long; glabrous; fertile stamens 10, 5 subequalling petals, alternate ones ½ the length of petals, unequally connate at base for 1–3 mm, inner surface tomentose, lacinate rim projecting above point of adnation, filaments slender, anthers linear-oblong, ca. 2 mm long on longer stamens, ca. 1.5 mm long on shorter stamens; pollen spheroid, inaperturate, sexine reticulate with blunt, spinelike infratectal processes; gynoecium subequalling petals, tomentose, gynophore subequalling style, stigma capitate. Fruit linear, apiculate with persistent style, 8–10 cm long, ca. 1.5 cm wide, dark brown, tomentose, gynophore 0.5–1.0 cm long; seeds not seen.

Bauhinia seleriana occurs in deciduous forests in southern Mexico, Guatemala, and Honduras at elevations from 700 to 1,500 m. It flowers from April to October.

This species is distinguished from other Middle American species of the genus with ten fertile stamens by the hirsute young branches, inflorescences, and undersurface of the leaves. It is most closely related to *B. andrieuxii* from which it is distinguished by larger leaves and conspicuously hirsute parts. Also, *Bauhinia seleriana* is found in forests while *B. andrieuxii* is in open deciduous scrub.

Local names for this species in Guatemala are "Pata de Javalin" and "Nam-nam-te" and in Honduras "Pata de Buey."

Representative specimens: MEXICO. CHIAPAS: Along Mexican Highway 190, 3 mi. S of La Trinitaria, *Breedlove 14485* (NY). OAXACA: Ca. 3 km to the NE of Laollaga, *Téllez & Magallanes 233* (MEXU, MO). GUATEMALA. HUEHUETENANGO: Between Nenton and Las Palmas, *Steyermark 51582* (F, US). ZACAPA: Loma El Picacho, above Santa Rosalia, *Steyermark 42730* (F, NY, US). HONDURAS. CHOLUTECA: 6 km SW of Panamerican Highway, *Harmon & Fuentes 5962* (UMO). EL PARAÍSO: Along Río California, Sierra de la Villa Santa, *Williams & Molina 10479* (F, MO, UC, US, VT). FRANCISCO MORAZÁN: Along Quebrada Suyapa, near Suyapa, *Molina 553* (F, MO, US).

26. **Bauhinia subrotundifolia** Cav., Icon. 5: 4. 1799. *Casparia subrotundifolia* (Cav.) H.B.K. ex Jackson in Index Kew. 1: 449. 1895, nom. inval. *Casparia subrotundifolia* (Cav.) H.B.K. ex Britt. & Rose, N. Amer. Fl. 23: 213. 1930. TYPE: Mexico. Guerrero: Vicinity of Acapulco, *Nee s.n.* (holotype, MA, not seen; fragment of holotype, F; photograph of holotype, F, MO, US).

Bauhinia lunaria Cav., Icon. 5: 4. 1799. *Casparia lunaria* (Cav.) H.B.K. ex Jackson in Index Kew. 1: 449. 1895, nom. inval. *Casparia lunaria* (Cav.) H.B.K. ex Britt. & Rose, N. Amer. Fl. 23: 213. 1930. TYPE: Mexico. Guerrero: Vicinity of Calavan and Acapulco, *Nee s.n.* (holotype, MA, not seen; fragment of holotype, F; photograph of holotype, F, MO, US).

Bauhinia rotundifolia Pers., Syn. Pl. 1: 455. 1805, nom. illeg. New name for *Bauhinia subrotundifolia* Cav.

Mandarus rotundifolius (Pers.) Raf., Sylva Tellur. 122. 1838.

Casparia oaxacana Britt. in Britt. & Rose, N. Amer. Fl. 23: 212. 1930. *Bauhinia oaxacana* (Britt.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 159. 1956. TYPE: Mexico. Oaxaca: Between Tequisistlán and Jalapa, *Seler 1687* (holotype, NY; isotype, GH).

Bauhinia subrotundifolia var. *salina-cruzana* Wunderlin, Southwest. Natur. 13: 104. 1968. TYPE: Mexico. Oaxaca: Salina Cruz, *Deam s.n.* (holotype, F).

Shrub or small tree up to 4(–7) m tall; branches densely short-pilose when young, soon glabrate. Leaves chartaceous, suborbicular, usually broader than long, bilobate for ca. ½ their length, lobes slightly divergent, 2–4 cm long, 3–6 cm wide, base cordate to rarely rounded, apex of lobes rounded, margins smooth or slightly crisped, upper surface glabrous, lower surface pilose or strigose, (5–)7-nerved; petiole 1.5–2.5 cm long, slightly canaliculate, pilose to glabrate; stipules broadly lanceolate, ca. 1.5 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection ca. 1.5 mm long, others minute. Inflorescences racemose, terminal, or frequently subterminal and axillary, 10–30-flowered, rachis densely pilose or strigose, buds linear-oblong, 1.0–1.5 cm long, densely pilose with tan or whitish hairs, occasionally densely strigose, free tips minute; bract linear-lanceolate, ca. 1 mm long; bracteoles similar, but smaller than bract; pedicel slender, 0.5–1.0 cm long, pilose with tan or whitish hairs, occasionally strigose; hypanthium cyathiform, ca. 1 mm long; calyx spathaceous at anthesis; petals 5, subequal, white, 1.0–1.5 cm long, blade elliptic, equalling or shorter than claw, 1–2 mm wide, sparsely pilose, claw pilose; fertile stamen 1, slightly exceeding petals, filament slender, slightly arcuate, sparsely pilose at base, connate with staminodes, anther oblong, ca. 1.5 mm long, glabrate; staminodes 9, subequal, 5–7 mm long, connate for ½ or more their length, pilose below, abortive anthers present or more commonly absent; pollen spheroid, 3-colporoidate, sexine striato-reticulate; gynoecium subequalling fertile stamen, slightly arcuate, ovary and gynophore densely pilose, style sparsely pilose to glabrate, gynophore subequalling style, stigma small, capitate, slightly differentiated from style. Fruit linear, apiculate with persistent style, 6–10 cm long, 1–2 cm wide, light brown, short-pilose; seeds suborbicular, 7–10 mm long, 6–8 mm wide, brown, funicular aril-lobe scars subequal, ca. 3 mm long.

Bauhinia subrotundifolia occurs along the southwestern coast of Mexico from Jalisco southeast to Oaxaca in dry woods at elevations from near sea level up to 60 m. It flowers from October to March.

This species is most closely related to *B. pringlei* and *B. pes-caprae* from which it is distinguished by smaller, suborbicular leaves bilobate to about their middle. It is further distinguished from *B. pringlei* by pilose petals and from *B. pes-caprae* by always erect rather than reflexed flower buds.

Representative specimens: MEXICO. COLIMA: Between Colima and Armenia, *Delgradillo 31* (MEXU). GUERRERO: Acapulco and vicinity, *Palmer 398* (A, F, GH, MICH, MO, NY, UC, US). JALISCO: Coastal plain near highway to Autlán, 5 mi. N of Bahia Navidad, *McVaugh 20901* (MICH). MICHOACÁN: Aquila-Cofradía del Mar, *Hinton et al. 16217* (IJ, LL, MICH, NY, UC, US). OAXACA: Near Tehuantepec, *Alexander 236a (2387)* (MICH, NY, US).

27. Bauhinia ungulata L., Sp Pl. 374. 1753. *Cansenia ungulata* (L.) Raf., Sylva Tellur. 122. 1838. *Pauletia ungulata* (L.) Schmitz. Bull. Jard. Bot. Nat. Belg. 43: 393. 1973. TYPE: *Herb. Miller* (holotype, BM, not seen).

Pauletia inermis Cav., Icon. 5: 6. 1799. *Bauhinia inermis* (Cav.) Pers., Syn. Pl. 1: 455. 1805; non Forsk., 1775; nec Perr., 1824; nec Billb. ex Walp., 1843. TYPE: Mexico. Guerrero: *Herb. Cavanilles* (holotype, MA, not seen).

Bauhinia cavanillei Millsp., Publ. Field Colombian Mus., Bot. Ser. 1: 364. 1898. Based on *Pauletia inermis* Cav.

Only names applying only to Middle American material are listed here. Additional names based on South American material will undoubtedly be placed in synonymy of this highly variable species when comprehensive study of the entire complex has been made.

Shrubs or small trees up to 7 m tall; branches densely brown strigose when young, soon glabrate. Leaves chartaceous, ovate to elliptic, bilobate to ca. middle, 5–12(–17) cm long, 3–8(–15) cm wide, base cordate to rounded, apex of lobes acute to rounded, upper surface glabrous, lower surface strigose or tomentellous, conspicuously glandular with medially attached boat-shaped glandular hairs, 7–9-nerved; petiole 1–3 cm long, slightly canaliculate, tomentellous; stipules ovate, ca. 1.5 mm long, caducous; adpetiolar intrastipular excrescence enlarged and forming a subulate projection up to 1.5 mm long, others

minute. Inflorescences appearing racemose through reduction of terminal leaves, consisting of 10–30 pairs of flowers produced at ends of branches, rachis tomentose to tomentellous, buds linear-oblong, subclavate, 4–5 cm long, tomentose to tomentellous, apex apiculate with short connate tips or rounded; bract ovate to lanceolate, 2–4 mm long; bracteoles similar to bract; peduncles up to 2 mm long; pedicels 0.5–1.5 cm long, tomentose to tomentellous; hypanthium short tubular, 8–15 mm long; calyx splitting to hypanthium into 5 lobes or lobes partly connate, curled, and reflexed at anthesis, inner surface white or cream; petals 5, subequal, white, blade narrowly linear to filiform, 2–3 cm long; stamens 10, equalling or exceeding the petals, alternate ones slightly shorter, slightly spreading, filaments slender, reddish, connate at base for 3–4 mm, sparsely pilose especially on connate portion with reddish hairs, anthers 9–12 mm long, glabrous; pollen spheroid, 3-colpate, sexine reticulate with clavate supratectal processes; gynoecium subequalling stamens, ovary tomentose, gynophore glabrate, subequalling style, style tomentellous, stigma oblique, differentiated from style. Fruit linear, apiculate with persistent style, 7–20 cm long, 0.7–1.3 cm wide, dark brown, puberulent, gynophore 2–3 cm long, glabrate; seeds oblong to suborbicular, 5–7 mm long, 4–5 mm wide, surface dull, dark brown, funicular aril-lobe scars subequal, 2–5 mm long.

In Middle America *B. ungulata* ranges from southern Mexico south to Panama. In western Mexico it occurs north as far as Sinaloa and in eastern Mexico it reaches Veracruz. The species is unreported from Honduras but is to be expected there. Outside Middle America this species is native to Colombia, Venezuela, Guyana, Peru, Brazil, Bolivia, and Paraguay. The species occurs in open deciduous forests, frequently in disturbed sites, at elevations from near sea level up to 1,300 m but is most common below 500 m. Flowering occurs throughout the year, but most commonly from October to March. The species is bat-pollinated.

Bauhinia ungulata is distinguished from other decandrous, unarmed *Bauhinia* species in Middle America by linear or subclavate flower buds in pseudoracemose inflorescences, and by narrow petals. It is allied to *B. multinervia* but has much smaller buds and fruits. *Bauhinia ungulata* is one of about 50 species in a complex centered in southern Brazil. This complex is currently under investigation by the author.

The local names for this species in Belize are "Pie de Vaca," in Costa Rica, Guatemala, and El Salvador "Pie de Venando," and in Venezuela "Pata de Vaca"; and in Mexico it is known by the Spanish names "Pata de Vaca" and "Pata de Venado" as well as the Mayan name "Chakts'ulubtok'."

Representative specimens: MEXICO. CAMPECHE: Ca. 16 km SE of Champotón, *Taylor & Taylor 12668* (MO, US). CHIAPAS: Escuintla, *Matuda 60* (MICH, MO, NY, US). GUERRERO: Santo Tomás, Cerrito de Valle, *Mexia 8932* (F, MO, NY, UC, US). JALISCO: S of Puerto Vallarta, *Mexia 1124* (F, MICH, MO, NY, UC, US). MÉXICO: Ixtapan, *Hinton 5297* (NY, US). MICHOACÁN: Ca. 45–48 km S of Arteaga, 12–15 km S of Playa Azul, *McVaugh 22572* (DUKE, MICH, UC, US). NAYARIT: 21 mi. E of San Blas, between Navarrete and Tepic, *Rudd et al. 3030* (MO, US, WIS). OAXACA: Ca. 15 km SW of Santa María Zacatepec, *McVaugh 22225* (DUKE, MICH, UC, US). QUINTANA ROO: Km 160 along Mérida-Valladolid road, *Moreno 396* (MEXU). SINALOA: Rosario, *Rose et al. 14512* (US). TABASCO: Villahermosa, *Juzepczuk 1919* (F, K). VERACRUZ: La Purga, *Greenman 277* (F, GH, UC, US). YUCATÁN: Chichankanab, *Gaumer 2262* (F, MO, NY, US). GUATEMALA. ESQUINTLA: Near Esquintla, *Hayes s.n.* (US). HUEHUETENANGO: Canyon tributary to Río Trapichillo between Democracia and Chamuchu Canyon, *Steyermark 51279* (F). PETÉN: La Libertad and vicinity, *Aguilar 342* (MICH, MO, NY). RETALHULEU: Río Samala, *Shannon 533* (US). SANTA ROSA: Region of La Sepultura, W of Chiquemulilla, *Standley 79312* (F, MO). SOLOLÁ: Patalul, *Holway 194* (US). BELIZE. CAYO: Pine Ridge, Duck Run, *Bartlett 11554* (MICH, NY, US). EL SALVADOR: AHUACHAPÁN: Atiquiozoya, *Calderón 2442* (F, NY). CHALATENANGO: Along Tujutla Creek, highway to La Palma, *Molina & Montalvo 21572* (F, NY). LA LIBERTAD: 8 mi. NW of La Libertad, *Wunderlin 5043* (MO). LA UNIÓN: Vicinity of La Unión, *Standley 20688* (NY, US). MORAZÁN: NW of San Miguel, *Tucker 480* (F, MICH, UC, US). SANTA ANA: Vicinity of Santa Ana, *Standley 19687* (F, MO, NY, US). SAN SALVADOR: Tonacetepeque, *Standley 19470* (NY, US). SAN VICENTE: 3 mi. W of Río Lempa near San Nicolás Lempa, *Wunderlin 5032* (MO). SONSONATE: Ca. 3–5 mi. NW of Sonsonate, *Wunderlin 5045* (MO). NICARAGUA. CARAZO: W bank of the Río Escalante at the Carazo-Rivas border 1 km from the Pacific coast, *Neill 1295* (MO). GRANDE: Grande, *Levy 366* (P). LEÓN: W of Quebrada Las Ruedas and along stream, NW of El Tránsito, *Stevens 5441* (MO, USF). MANAGUA: Along Route 10 between Managua and Masachapa, 10 mi. S of junction with Route 12, *Croat 43701* (MO, USF). COSTA RICA. ALAJUELA: Orotina, *Holway 315* (US). GUANACASTE: Ca. 20–30 km W of Liberia, *Williams et al. 26487* (F, NY). PUNTARENAS: Between Quebrada Grande and Quebrada Guajiniquil near Buenos Aires, *Molina et al. 18145* (F, NY). PANAMA. CANAL ZONE: Vicinity of San Feliz, *Pittier 5281* (NY, US). CHIRIQUÍ: Quebrada Las Canas, 9 km N of David, *Partch 69-66*

(MO). DARIÉN: Patino, *Duke 10545* (MO, NY). HERRERA: 4 mi. S of Los Pozos, *Tyson 2648* (MO, SCZ, US).

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 inermis Billb. ex Walp. *124*
 inermis (Cav.) Pers. *124*
 inermis Forsk. *124*
 inermis Perr. *124*
 jenningsii P. Wilson *100, 110*, **112-113**, *119*
 jermyana (Britt.) Lundell *114*
 jucunda Brandeg. *100, 112*, **113-114**
 kalbreyeri Harms *119*
 lamarkiana DC. *108*
 latifolia Cav. *108*
  [var.] *beta* Hook. & Arn. *108*
 leptopetala DC. *117*
 ligulata Pittier *119–120*
 longiflora (Bong.) Steud. *117*
 longiflora Rose *117*
 lunaria Cav. *123*
 lunarioides A. Gray ex S. Wats. *100*, **114-115**, *121*

macranthera Benth. ex Hemsl. *100*, **115**, *121–122*
var. *grayana* Wunderlin *115*
macrophylla Poir. *104*
megalandra Griseb. *116*
mexicana Vog. *108*
miranda Pittier *101*
mollicella Blake *101*
mollifolia Pittier *101*
monantha (Britt. & Rose) Lundell *121*
multinervia (H.B.K.) DC. *101*, **115-116**, *125*
oaxacana (Britt.) Standl. *124*
palenquensis Lundell *122*
panamensis Spreng. *117*
pansamalana Donn. Sm. *100, 103*, **116-117**
paradisi Standl. & L. O. Williams *123*
parvifolia Hochst. ex Field. & Gard. *117*
parvifolia Seem. *117*
parvifolia Teijsm. & Binn. *117*
pauletia Pers. *100, 102*, **117-118**
peninsularis Brandeg. *108*
pes-caprae Cav. *99–100*, **118-119**, *121, 124*
petensis Lundell *110*
petiolata (Mutis ex DC.) Triana ex Hook. f. *99, 101, 103*, **119**
picta (H.B.K.) DC. *101*, **119-120**
platypetala Benth. ex Hemsl. *105–106*
platypetala Burch. ex Benth. *106*
porrecta Sw. *108*
pringlei S. Wats. *100*, **120-121**, *124*
purpusii (Britt.) Lundell *121*
racemifera Desv. *108*
ramosissima Benth. ex Hemsl. *101, 115*, **121-122**
retifolia Standl. *115*
retusa Ham. ex Roxb. *108*
retusa Poir. *108*
rotundata Mill. *101*
rotundifolia Pers. *123*
rubeleruziana Donn. Sm. *100, 109*, **122-123**
rufescens Lam. *108*†
runyonii (Britt. & Rose) Standl. *121*
schlechtendaliana Mart. & Gal. *108*
schultzei Harms *101*
seleriana Harms *101, 103*, **123**
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spinosa Poir. *117*
subrotundifolia Cav. *100, 119, 121*, **123-124**
var. *salina-cruzana* Wunderlin *124*
tarapotensis Benth. *99*†
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ungula Jacq. *101*
ungula Willd. ex Steud. *101*
ungulata L. *99, 101, 116*, **124-126**
uniflora Hassler *121*†
uniflora S. Wats. *121*
unilateralis Britten & Baker *107*
versicolor Bertol. *108*
Bauhinia Raf. *99*
Cansenia Raf. *99*
ungulata (L.) Raf. *99, 124*
Casparia Kunth *99*
amblyophylla (Harms) Britt. & Rose *108*
aurita (Ait.) Griseb. *108*
calderonii Rose *104*
confusa (Rose) Britt. & Rose *108*
congesta Britt. & Rose *114*
coulteri (Macbr.) Britt. & Rose *106*
deserti Britt. & Rose *106*
dipetala (Hemsl.) Britt. & Rose *107*
divaricata (L.) H.B.K. ex Jackson *107*
divaricata (L.) H.B.K. ex Britt. & Rose *107*
furcata (Desv.) Jackson *108*
jenningsii (P. Wilson) Britt. & Rose *112*
jermyana Britt. *114*
jucunda (Brandeg.) Britt. & Rose *113*
latifolia (Cav.) H.B.K. ex Jackson *108*
lunaria (Cav.) H.B.K. ex Jackson *123*
lunaria (Cav.) H.B.K. ex Britt. & Rose *123*
lunarioides A. Gray ex Britt. & Rose *115*
macranthera (Benth. ex Hemsl.) Britt. & Rose *115*
mexicana (Vog.) Britt. & Rose *108*
monantha Britt. & Rose *121*
oaxacana Britt. *124*
pansamalana (Donn. Sm.) Britt. & Rose *116*
peninsularis (Brandeg.) Britt. & Rose *108*
pes-caprae (Cav.) H.B.K. *99, 118*
porrecta (Sw.) Kunth ex Griseb. *108*
porrecta (Sw.) H.B.K. ex Jackson *108*
pringlei (S. Wats.) Britt. & Rose *120*
purpusii Britt. *121*
ramosissima (Benth. ex Hemsl.) Britt. & Rose *121*
retifolia (Standl.) Britt. & Rose *115*
rubeleruziana (Donn. Sm.) Britt. & Rose *122*
runyonii Britt. & Rose *121–122*
schlechtendaliana (Mart. & Gal.) Britt. & Rose *108*
spathacea (DC.) Britt. & Rose *108*
speciosa Linden ex Hook. f. *119*
subrotundifolia (Cav.) H.B.K. ex Jackson *123*
subrotundifolia (Cav.) H.B.K. ex Britt. & Rose *123*
unguicularis (Benth. ex Hemsl.) Britt. & Rose *121*
uniflora (S. Wats.) Britt. & Rose *121*
unilateralis (Britten & Baker) Britt. & Rose *107*
versicolor (Bertol.) Britt. & Rose *108*
Mandarus Raf. *99*
divaricatus (L.) Raf. *99, 107*
pes-caprae (Cav.) Raf. *118*
rotundifolius (Pers.) Raf. *123*
Pauletia Cav. *99*
aculeata Cav. *117*
glandulosa H.B.K. *101*
glaucescens H.B.K. *116*
inermis Cav. *99, 124*
multinervia H.B.K. *119*
picta H.B.K. *119*
ungulata (L.) Schmitz *124*
Perlebia Mart. *99*
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Perlebia Schmitz *99*
Schnella caudigera (Blake) Pittier *119*

A GUIDE TO COLLECTING BAMBOOS[1]

THOMAS R. SODERSTROM[2] AND STEPHEN M. YOUNG[3]

ABSTRACT

Because of their specialized nature and infrequency of flowering, bamboos are seldom collected. An illustrated guide is presented, showing which parts—especially vegetative—should be collected for a proper herbarium specimen. Instructions are also given on the preparation of preserved material in liquid and on the composition of the notes and label to accompany the collection.

Plant collectors are so accustomed to limiting their activities to plants in flower that sterile specimens are generally avoided. In the case of bamboos, which often flower only at intervals of many years, the collector rarely encounters them in the reproductive state. Both this fact and the complexity of the plant itself account for the relatively poor representation of bamboo specimens in herbaria. However, because of this very propensity of bamboos to flower seldom, taxonomic studies on the group have relied heavily on sterile characters. In fact, a complete vegetative collection is often sufficient to allow identification to the generic, if not specific, level.

We encourage collectors to make specimens of any bamboo they encounter, vegetative as well as flowering. We realize the importance of knowing how to look at the living plant, what structures are most significant taxonomically, and what information to record and parts to collect. With this in mind we have prepared a checklist of the observations to be made and representative parts to collect.

In the following checklist we have given, under General Data, the facts that should be recorded for any collection. Once these data have been recorded, the collector should survey the bamboo clump and analyze its major components, each of which is treated separately in the checklist: culms, culm leaves, branches, branch leaves, inflorescences, and rhizomes. Only rarely will all parts be present at the same time, for the strictly vegetative plant will lack flowers and the plant in flower may already have shed its leaves and lack new culms.

Under each heading we have listed, in a logical sequence, the observations that should be recorded, starting with overall or general characteristics and continuing with more specific ones, giving examples where appropriate. For instance, the interior of the culm may be solid or hollow with a thick or thin wall; if the latter it may contain a fine powder on the inner walls or be filled with liquid. The characters listed are examples of the most common kinds. Thus, under "Internode Color," additional variations may be found, such as "green mottled with purple." We have illustrated the most important features and at the end of each section we have suggested what parts to collect. For all measurements we recommend the metric system.

The final result of a complete collection should be adequate samples of all parts of the plant, including those that can be processed in the plant press, such as the branch leaves, and those that must be dried and tagged separately, such as culm sections or branch complements. In addition to the plant collection, a full set of notes will supplement the actual material gathered. The label that accompanies the mounted specimens must be concise and contain the most complete information possible, not including anything that can be seen on the herbarium specimen itself. Figure 6 is an example of such a label.

The general collector will naturally confine most of his work to data collecting and the gathering of only those parts that can be accommodated in a plant press and later mounted in the herbarium. The more serious student will want to collect bulky parts as well, although making such a collection often requires up to several hours. The researcher who will undertake anatomical, morphological, and cytological studies in the laboratory will need to collect further ma-

[1] We are grateful to Alice R. Tangerini whose skillful renditions of the bamboo figures will be more helpful to the collector than any amount of text.

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terial in liquid preservative and can follow the methods and use the formulas presented at the end of this paper.

We recommend that the collector of bamboo include in his equipment a pair of heavy gloves to protect against spines and irritating hairs and a machete or similar cutting tool for severing the culms, along with a cross-cut saw for trimming them neatly. A good pair of pruning shears is indispensable.

Photographs, especially of the habit and habitat, greatly enhance any collection. A wide-angle lens is especially useful for photographing the habitat or an entire clump from close range and a macro lens for recording carriage of the foliage and details of structures such as buds and developing branches, inflorescences and spikelets.

Bamboo Collecting Checklist

A. General Data.
   1. *Date.*
   2. *Locality:* use of latitude and longitude is recommended.
   3. *Elevation.*
   4. *Habitat:* characterize the vegetation and substratum.
   5. *Common Names and Uses:* inquire locally.

B. Components of the Bamboo Plant.
   1. *Culms.*
      a. *General Characteristics.*
         1) *Spacing:* close together and forming clumps (if so, state diameter of clump and estimate number of culms included); widely separated and not forming discrete clumps.
         2) *Habit:* strictly erect; erect and arching over; decumbent; clambering; vinelike (climbing or hanging).
         3) *Size:* height or length; diameter.
      b. *Node.*
         1) *Occurrence:* solitary (Fig. 1a) or in close succession (Fig. 1g).
         2) *Shape* (in longitudinal section): sides parallel (Fig. 1a); narrower below and widening above (Fig. 3d).
         3) *Architecture:* single nodal line present, this horizontal (Fig. 3f) or dipping (Fig. 3i); nodal line plus nodal ridge present (Fig. 3d); girdle present (Fig. 3a).
         4) *Surface:* smooth; pubescent; beset with root primordia or root thorns (Fig. 3j).
      c. *Internode* (Fig. 1a).
         1) *Color:* green; bluish-green; green with white stripes; yellow with green stripes.
         2) *Surface:* glabrous; pubescent; glabrous on the lower part, becoming scabrous above; glaucous.
         3) *Shape in Cross Section:* round (Fig. 1e); sulcate (Fig. 1d); plano-convex (Fig. 3d).
         4) *State:* hollow (indicate wall thickness) (Figs. 1a, b); solid (indicate amount of pith) (Figs. 1c, e).
         5) *Contents* (when hollow): empty; powder on inside walls; filled with liquid.

To Collect: Two nodes and included internode (Fig. 1a). The culm may be split lengthwise. If culm is too long cut a shorter section and include only one node, but measure and record length of the internode.

   2. *Culm Leaves* (Fig. 2).
      a. *General Characteristics.*
         1) *Duration on Culm:* persistent; caducous; tardily deciduous.
         2) *Variability:* same shape throughout culm; thin and long at top of culm and wide and short at base of culm; becoming smaller toward top of culm.
         3) *Color and Pattern* (when fresh): mottled; striped.
         4) *Surface:* glaucous; densely covered with hairs; glabrous.
         5) *Texture:* hard; soft.
      b. *Blade.*
         1) *Posture:* erect (Figs. 2a, b, f); reflexed (Fig. 2d); horizontal (Fig. 2c).
         2) *Duration on Sheath:* remaining attached; falling.

To Collect: When possible, collect at least two culm leaves from that part of the culm where they are most representative in size and shape. If the leaves have already fallen, select from these. When the sheath is persistent cut it from the culm and press it flat, even though this may result in cracking and splitting.

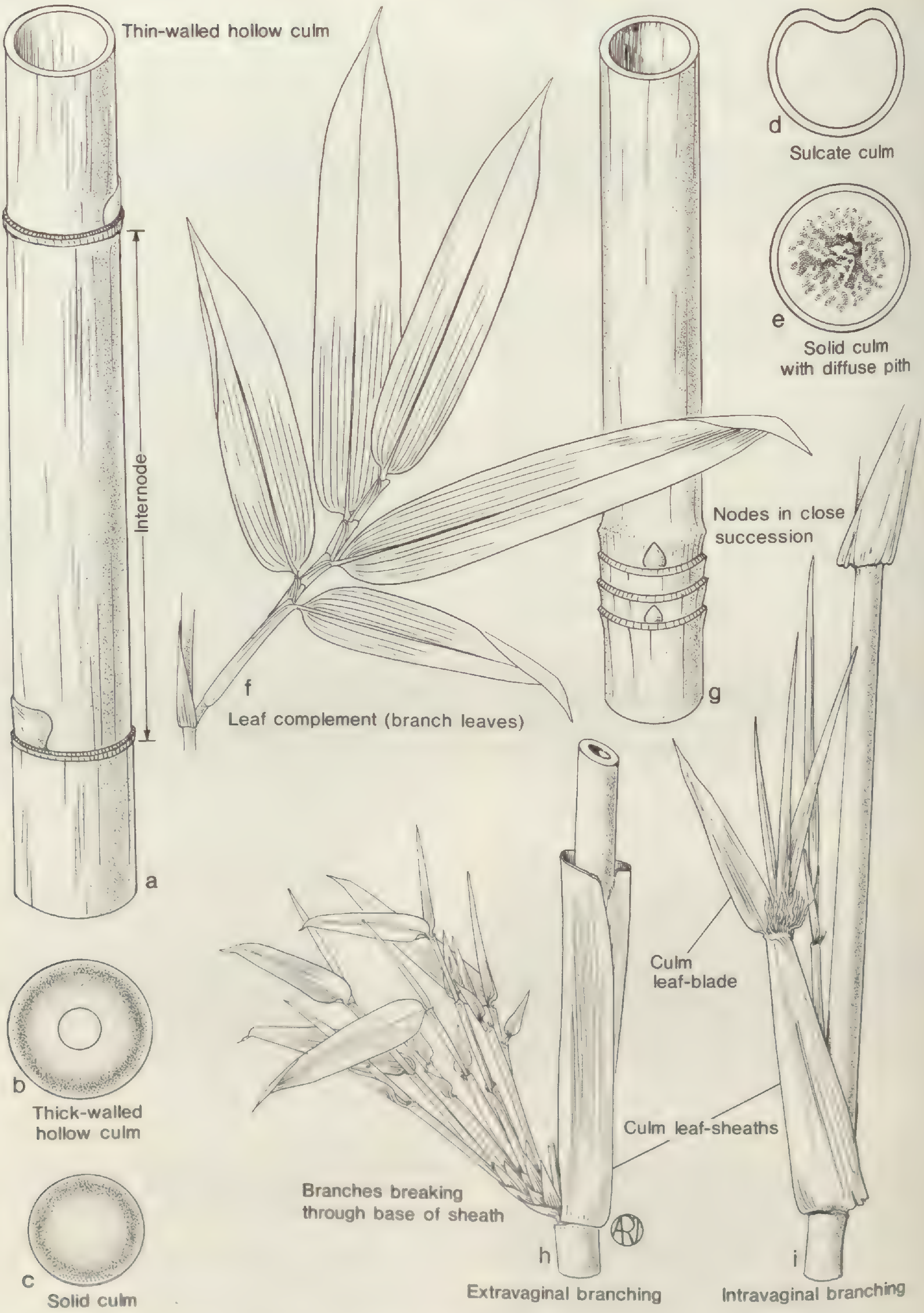

FIGURE 1. Culms, branching and branch leaves.

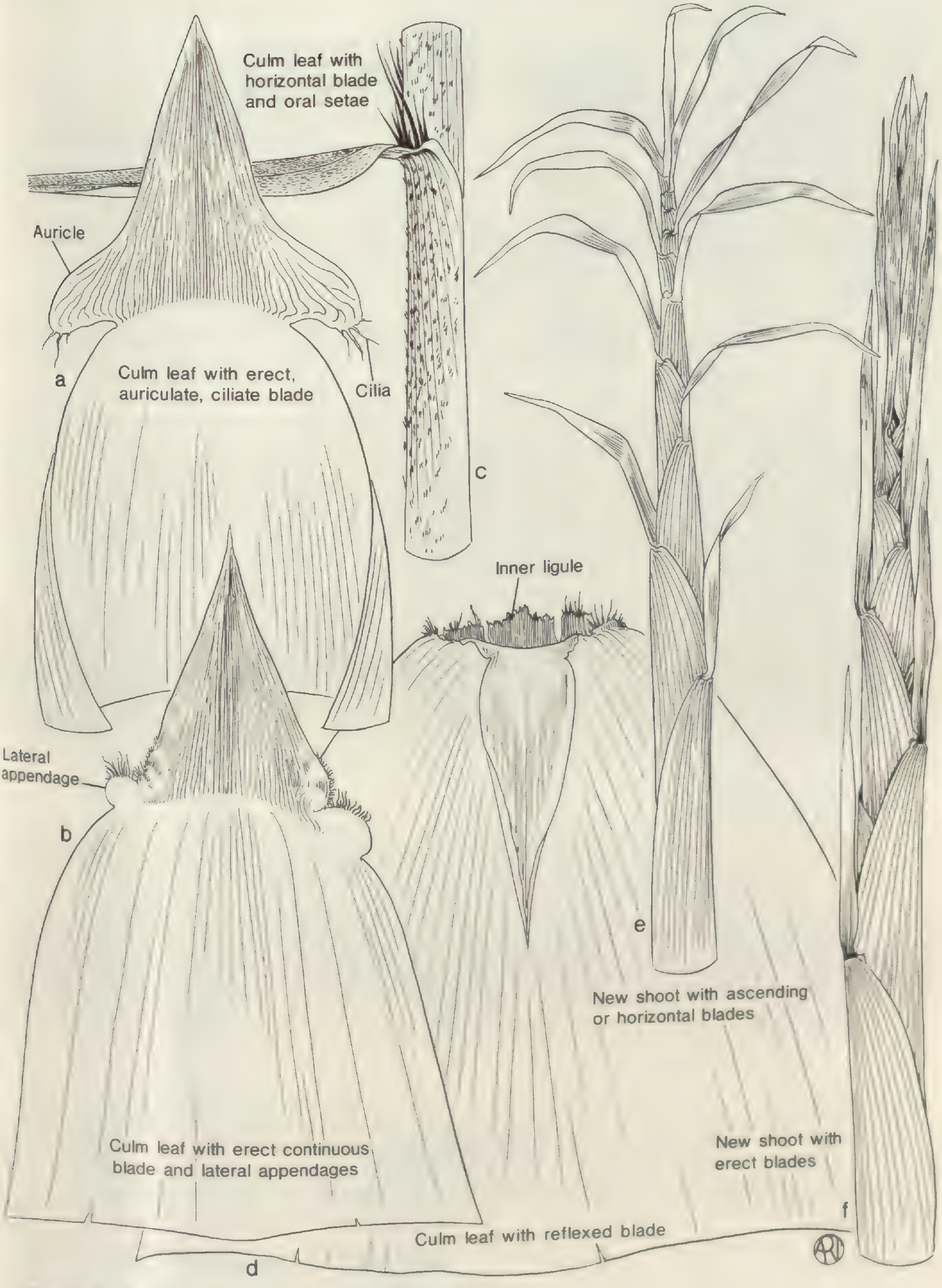

FIGURE 2. Culm leaves.

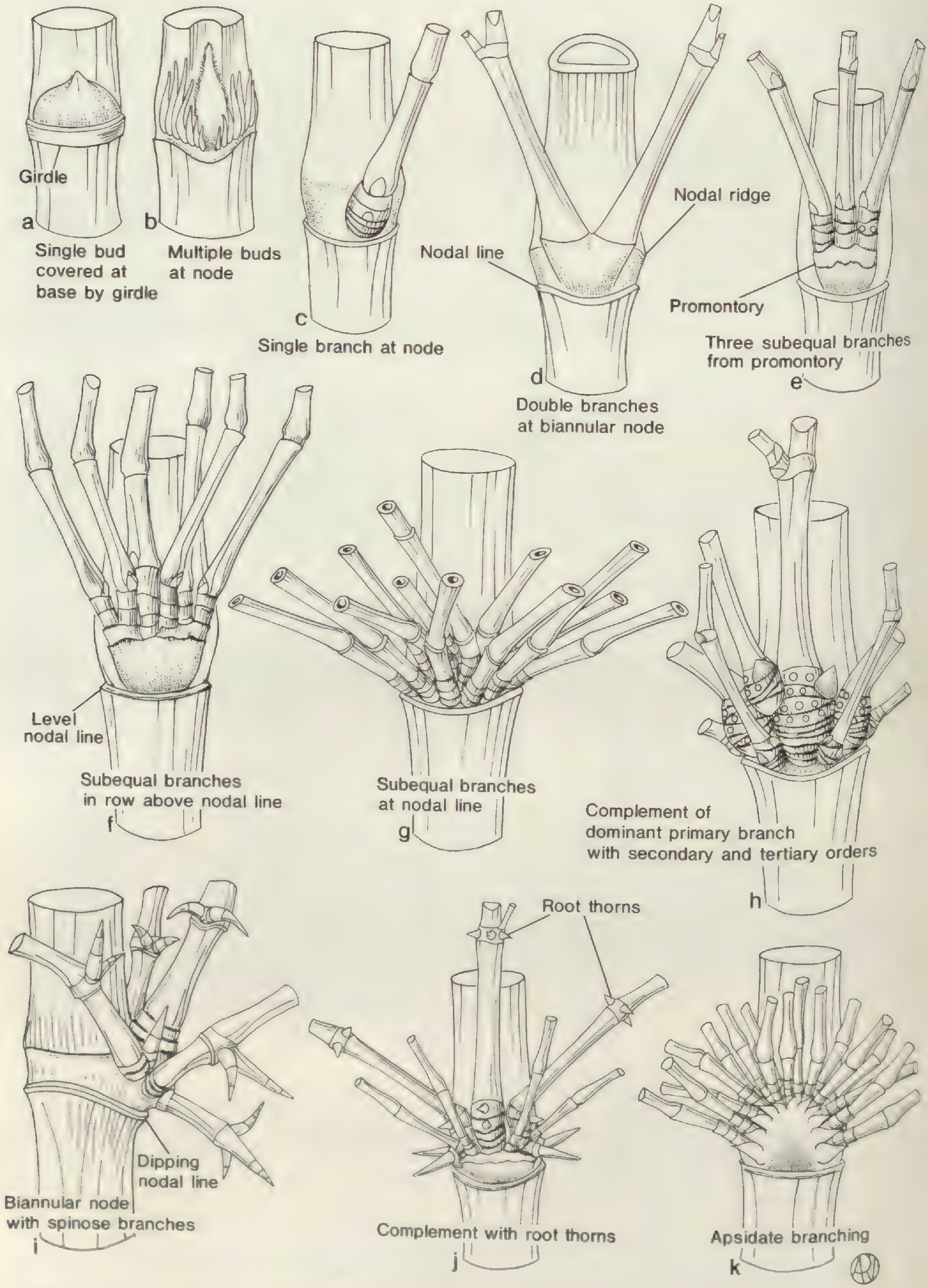

FIGURE 3. Nodes, buds, and branching.

FIGURE 4. Inflorescences.

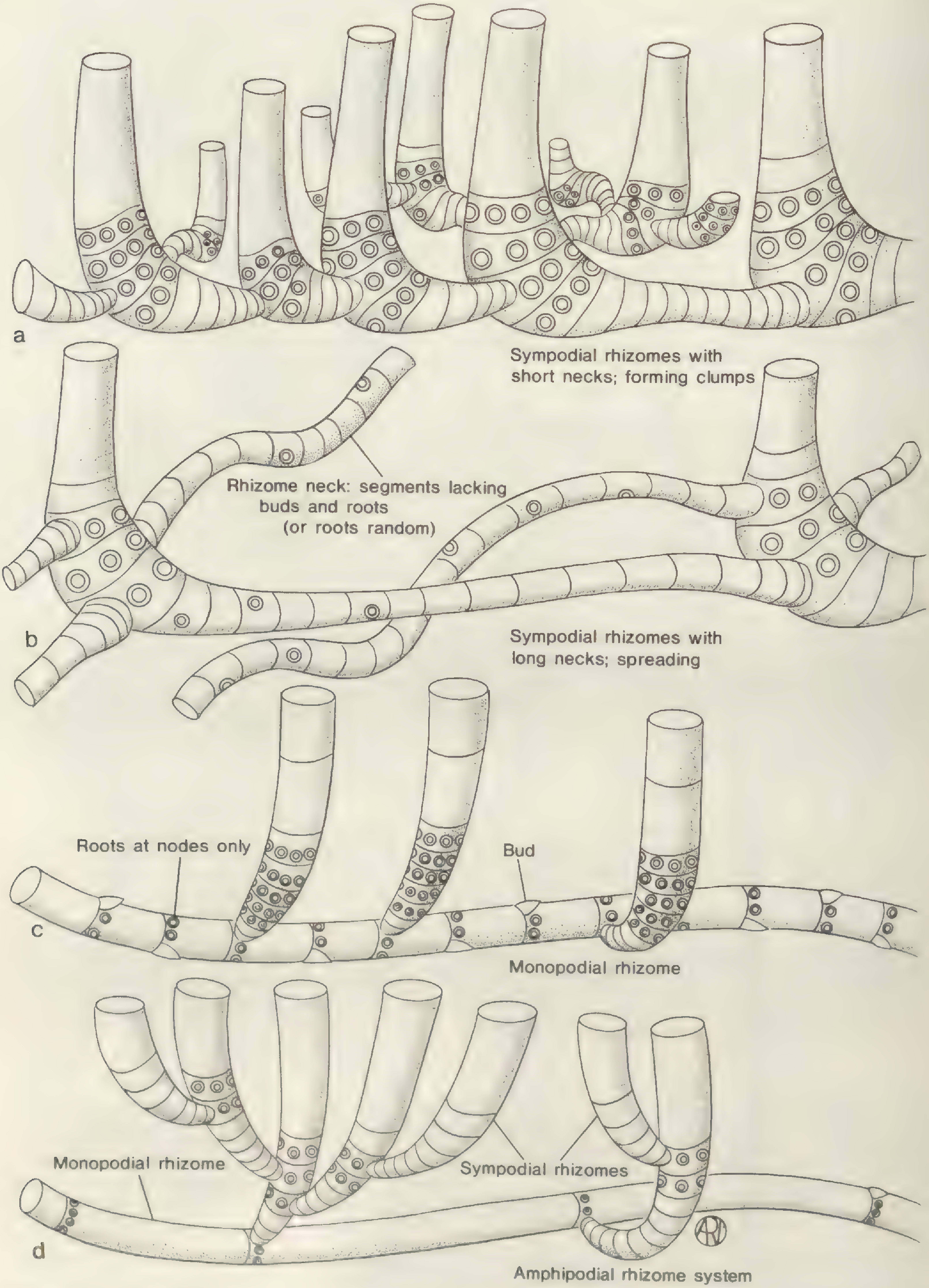

FIGURE 5. Rhizomes.

MEXICO

Olmeca recta Soderstrom

Veracruz: Mun. Catamaco, 10 Km N of Catamaco on road to Sontecomapan, 18°30′ N / 95°01′ W. Growing under tall trees in disturbed evergreen rain forest; common throughout the Tuxtla Range. Culms well separated from each other, 11–12 m tall, 4.5–5 cm diam., thin-walled, often filled with water, rotting easily. Rhizomes to 3 m long, running near surface of the soil. Culm leaf: sheath bluish-green, becoming pinkish-brown then stramineous; blade erect, deciduous, bright green. Branching: only from upper nodes, the branches intravaginal, arching out and becoming vinelike. Common name "Jimba."

Elev. 435 m
Thomas R. Soderstrom 2235 — 2 Oct. 1977

Collected under the auspices of the Smithsonian Institution and Colegio de Postgraduados, Chapingo, Mexico

FIGURE 6. Herbarium label for bamboo collection.

3. *Branches.*
   a. *General Characteristics.*
      1) *Occurrence:* upper nodes only; all nodes.
      2) *Habit and Length:* main branches elongated and vinelike; upper branches angled upward, lower reflexed.
      3) *Development:* intravaginal (Fig. 1i); extravaginal (Fig. 1h); both intra- and extravaginal.
   b. *Number and Arrangement:* single branches (Fig. 3c); 2 subequal branches (Fig. 3d); 3 or more subequal branches (Figs. 3e, f, g); 1 dominant with further branches from the node (Figs. 3h, i); 1 dominant branch (sometimes remaining as a bud) with smaller subsidiary branches below or around it (Fig. 3b, shown in bud stage); or in apsidate arrangement without a central branch (Fig. 3k).
   c. *Origin:* produced at nodal line (Figs. 3c, g, h); produced above the nodal line (Fig. 3f); produced from a specialized process (Figs. 3e, j, k).
   d. *Posture at Node:* appressed (Figs. 3f, k); horizontal (Fig. 3g); angled upward (Figs. 3c–f, h–k); angled downward (Fig. 3i).
   e. *Modifications:* developing as spines (Fig. 3i).

To Collect: Take a representative branch complement from mature or old culm, even from dead culms that show the features accurately. Cut culm ca. 5 cm above and below the node and trim branches to ca. 5 cm, at least including the first node. Large culm sections may be split in half to save space. As with culm sections, allow to air-dry and remove all sheaths.

4. *Branch Leaves* (Fig. 1f).
   a. *General Characteristics.*
      1) *Condition After Cutting:* wilting or curling immediately; remaining fresh.
      2) *Habit:* stiff, flexuous; erect; pendent.
   b. *Color:* green on both surfaces; lighter on one surface than the other; variegated.

To Collect: Leafy twigs, arranging the leaves to show both surfaces. Include leaves from young and old branches if there is a significant size difference. Press immediately to avoid curling. If this is not possible the material can be wetted and retained in a tightly secured plastic bag. Large leaves may require trimming and folding or dividing and pressing in more than one sheet.

5. *Inflorescences* (Fig. 4).
   a. *General Characteristics.*
      1) *Habit:* erect; lax; drooping.
      2) *Occurrence:* terminating leafy branches; occurring throughout a leafless plant.
   b. *Size:* length and width if larger than an herbarium sheet.
   c. *Color:* green; stramineous; purple.

To Collect: Flowering branches at all stages of development. When a flowering bamboo is found in the leafless state and leafy non-flowering clumps are encountered nearby, do not assume that the two are the same species. If uncertain, collect each plant under a separate number and cross-reference.

6. *Rhizomes* (Fig. 5).
   a. *General Characteristics.*
      1) *Length Between Culms and Diameter:* short and thick; long and slender.
      2) *Habit:* specialized as props for culm; running overground; running underground.
   b. *Occurrence of Buds on Rhizome Neck:* present (Figs. 5c, d); or absent (Figs. 5a, b).
   c. *Position of Roots:* at the nodal line only (Figs. 5c, d); at random (Fig. 5b).

To Collect: For running types collect a section of the rhizome ca. half a meter long. For clump-forming types collect 2–several rhizomes and sever culms ca. 15 cm above the ground. Air-dry the sample and remove all scales (sheaths).

C. Collections in Liquid Preservative.

1. *Morphological and Anatomical Studies:* parts of the plant can be preserved in FAA in the field and either stored this way or transferred to 70 percent ethyl alcohol, EtOH. FAA is prepared by mixing 90 parts of 50 percent EtOH, 5 parts of glacial acetic acid, H(Ac), and 5 parts of formalin. To make 1 liter, use 900 ml of 50 percent EtOH, 50 ml of H(Ac), and 50 ml of formalin. First add the H(Ac) to the EtOH and then mix in the formalin. After several days the solution undergoes esterification and emits a sweet smell, which indicates the solution is too old for fixing material.
2. *Plant Parts for Preservation.*
   a. *Branch Leaves:* the blades and portion containing the petiole and ligule are the important parts to collect. On small leaves cut the blade just above the base; on larger ones cut a section 3–5 cm long from the mid-portion of the blade, including the midvein. On exceptionally large blades cut a strip (3–5 cm wide) that includes the midvein and one side of the blade. For the petiole and ligule portion, cut the leaf just above the base of the blade and just below the apex of the sheath.
   b. *Buds at Different Stages of Development:* these are important in following the stages of development of the mature branches. Usually only one bud is present (Fig. 3a) but sometimes more than one occurs at a node (Fig. 3b). The base of the sheath is often thickened and remains as a ring, or girdle, around the bud (Fig. 3a). Any excess culm tissue from around the bud can be trimmed away.
   c. *Fleshy Fruits:* these may be collected in a separate bottle and sliced into sections if unusually large.
   d. *Roots:* sections ca. 2 cm long should be cut for preservation.
   e. *Seedlings:* only young ones, with the seed still attached, should be collected.
   f. *Culm Sections:* some may be preserved if they exhibit unusual colors or patterns, such as mottling or stripes that would be lost in air-drying.
3. *Cytological Studies:* young spikelets can be fixed in a 3:1 solution for 24 hours and then transferred to 70 percent EtOH and kept under refrigeration when possible. The 3:1 solution is made by mixing 3 parts of absolute EtOH and 1 part of H(Ac). Spikelets should be collected from inflorescences that are still covered by the subtending sheath or just beginning to emerge (Fig. 4h).

A GUIDE TO COLLECTING PANDANACEAE (*PANDANUS, FREYCINETIA,* AND *SARARANGA*)

Benjamin C. Stone[1]

The family Pandanaceae is paleotropical and consists of three genera, *Pandanus* L. ex Stickm. with the most species (over 600) and the widest distribution, from W. Africa eastward throughout the tropical areas to the Pacific Islands; *Freycinetia,* with about 180 species and the next largest distribution, from Ceylon (but not India, except the Andaman and Nicobar Islands) eastward through the Malesian area into the Pacific and New Zealand; and *Sararanga,* a restricted small genus of two species, one in the Philippines and the other in New Guinea and the Solomon Islands.

All species of *Freycinetia* are woody lianas; among these there occur some relatively large plants, with stems reaching perhaps 6–7 cm diameter and leaves of perhaps 150 cm length and a width of perhaps 10 cm; but most species are rather smaller and some are really quite small plants, the extreme perhaps being *Freycinetia elegantula* with leaves only 2–3 cm long. Both species of *Sararanga* are arboreous, branched, with rather massive leaves 200 cm long or more, and erect trunks. They have, unlike all other pandans, compound paniculate inflorescences that are pendulous and may be well over 100 cm long. The genus is readily recognized by its quadrifarious spiral phyllotaxy, and concomitant square-section inflorescence rachises. The flowers and fruits are also unique in the family, the latter being irregularly globular many-seeded berries. The true pandans, *Pandanus* species, have a rather wide range of form and size, with tall arboreous plants such as *Pandanus antaresensis* of New Guinea, which may reach 33 m height and have massive proproots 10 m long and 20 cm thick, at one extreme, and diminutive shrubs such as *Pandanus herbaceus, P. toei,* or *P. unguiculatus,* which have short slender stems reaching at most 2 m height, and 2–3 cm or less in diameter (and in examples such as *P. toei,* are cespitose with little stem development) at the other extreme. Besides these examples, pandans have developed into epiphytic shrubs, some with a pseudo-lianous type of growth, others cespitose and "stemless" and most of these are small shrubs, although one species (*P. epiphyticus*) is, apart from its reduced stem, quite massive.

The family is important in several regions wherein it has developed a high degree of endemism and contributes to the fundamental structure and physiognomy of the vegetation. In other regions its presence is limited to coastal areas. Only in the Philippines, New Guinea, and the Solomon Islands can all three genera be found occurring together. Outlying posts of the family include New Zealand, which has only *Freycinetia,* and only one species; and Sao Thomé Island (off Angola, W. Africa), where one species of *Pandanus* occurs. Central areas of endemism are Madagascar, which has only the genus *Pandanus* but about 100 endemic species; Thailand, which has both *Freycinetia* (but only two or three species) and *Pandanus,* the latter with perhaps over two dozen species; Malaya, with eight species of *Freycinetia* and about fifty of *Pandanus*; Borneo, with two dozen species of *Freycinetia* and more than fifty of *Pandanus*; the Philippine archipelago, with about the same numbers of both genera as Borneo; New Guinea, with probably about 60 species of *Freycinetia* and 70 or more of *Pandanus*; the Solomon Islands, with about 23 species of *Freycinetia* and 28 species of *Pandanus*; and New Caledonia, with about 14 species of *Freycinetia* and 21 species of *Pandanus.* Some important secondary centers include Australia, especially Queensland, with only four species of *Freycinetia* but a somewhat richer *Pandanus*-flora (possibly 15–20 species); Fiji; Mauritius; the Seychelles; Burma and the Himalayan foothills; Sumatra; and East Africa. Besides these, several small regions have one or a few local endemic species, usually of *Pandanus* to the exclusion of the other genera; examples are Lord Howe Island, Christmas Island (Indian Ocean), Hainan, etc.

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MORPHOLOGY

Basic habit has been described above. In all species, the leaf is simple, usually more or less elongated, often long linear-attenuate, but (mostly in *Freycinetia*) sometimes subelliptic to ovate. The margins of the leaf are usually denticulate, as is the midrib on the undersurface. In *Pandanus* (only) many species also have teeth (spinules, aculeations, denticuli, prickles) on the upper (ventral) leaf apex, along the two pleats; their presence is a major taxonomic character and is a principal reason why good, intact material of leaf apices must be present in all pandan collections. The size, spacing, form, color, and other details of the leaf teeth are also of taxonomic importance. In *Freycinetia*, the leaf-sheath is elaborated by the presence of a pair of auricles, which are membranous flanges of the leaf-base; these are more or less distinct and taxonomically significant, and careful attention to obtaining good specimens is required. In *Pandanus*, such auricles are almost always lacking but a few species possess them and in any case good complete leaf-bases are a requisite for adequate representation in the herbarium. As the leaves are often very large (in a few cases, up to 9 m long and 21 cm wide), it is often impossible to collect more than a few. In fact, most herbarium material consists of a single leaf, or less, except in the case of very small plants such as *Pandanus herbaceus*. The collector must attempt to represent leaf variation in his collection. (Methods are described below.)

The trunk and proproots may furnish some taxonomically useful data, but are often either not collected, or may be difficult and bulky. Slabs of wood, with bark, from the main trunk, can be obtained, and segments of proproots. Certainly the habit, the branching pattern, and development, if any, of proproots should be noted in the form of sketches or photographs. In *Freycinetia*, aerial roots are either clasping or feeding (axillary); proproots (rigid ones) are not produced. Nor are there proproots in the *Sararanga* species. Epiphytes commonly produce feeding axillary roots.

The inflorescences are invariably terminal. However, they may terminate a normal leafy shoot, or a specialized lateral or axillary shoot. The latter differ from normal leafy shoots in possessing a reduced number of ordinary leaves, or in lacking such leaves, while bearing the usual scale leaves and bracts, and show the normal 2-ribbed prophyll at the base. Species of *Pandanus* and *Freycinetia* may have such lateral inflorescences (examples include *P. danckelmannianus* and *P. halleorum*, and *F. funicularis*). Therefore it is very important for the collector to represent, preferably by means of the collection itself, the inflorescence position. If this is impossible, drawings or photographs should document it. The inflorescences of *Sararanga* are always terminal.

The construction of the inflorescence varies with the species. However, all may be described as a branched or, rarely, an unbranched, spadix. The most important consideration is the strict unisexuality of the plants; a given individual is male or female and can therefore bear only one sexual kind of inflorescence. *One of the most important tasks of the collector, therefore, is to attempt to obtain both male and female inflorescences of any particular species.* Unfortunately, this is by no means easy. Staminate material is poorly represented in herbaria; but correlated staminate and pistillate materials judged or proven by the collector to represent the sexes of a single species are even rarer. Isolated staminate collections in themselves are useful, but may be unidentifiable. On occasion, they may (and have) represented unknown species, and some have been described and designated as type specimens. However, since the whole taxonomic system is based upon characters of the pistillate plants, such species are often fascinating but frustrating and may remain "incertae sedis" or even "nomina dubia" until the females are discovered. The role of the staminate material is however becoming increasingly important as more is learned of the micromorphology and anatomy, and in some cases can already be of critical significance in taxonomy; but good collections are still rare. One reason is the difficulty of locating staminate inflorescences. As flowering is seasonal in most pandans, while fruit development is a lengthy process, there is a much higher probability of finding pistillate trees with partly developed fruits, than there is of finding staminate specimens with fresh flowers at anthesis. The duration of a staminate inflorescence is usually only one to three days; while the flowering season may only be a week or two. In contrast, fruit development may take several months. Phenology of flowering in the pandans is still poorly known. However, there are certainly several patterns already in evidence. In some cases (*Pandanus fragrans*) flowering may be approximately every other month. In other cases, flowering may

be at intervals longer than one year. Many species are probably gregarious with synchrony in flowering, but the period may be very short. Robert Tucker in Queensland has reported that annual flowering in *Pandanus conicus* and *P. tectorius* is highly concentrated in a two-week period, with in fact most anthesis taking place in the same week. Much of the rest of the year, the plants appear to be sterile, except those that are gestating fruits. Such patterns of flowering mean that collectors often encounter flowering pandans at random and by chance, and find ripe flowering materials very much less commonly than unripe, or even ripe, fruits. However, it should be remembered that if staminate individuals are seen to be in flower (they are usually the more obvious, as the inflorescences are more lax and pendulous, and the white or colored spathes are noticeable), then it is highly likely that searching will reveal pistillate plants in the same locality also in flower. Such searches are of the greatest importance in linking staminate with pistillate collections to establish full knowledge of a species. But a caution must be noted: there are many localities in which several species of the same genus are sympatric and intermixed, and extreme care must be taken to establish *vegetative* similarities of the sexes. The danger of attributing flowering male and female plants to the same species, but in fact having material from males of one species and females of another, is quite serious.

The staminate inflorescences are spikelike. Usually, there are several spikes, each with an axillant bract, from the main rachis. In a few cases, the inflorescence is reduced to a single, apparently terminal spike, though there are always several bracts. (The bracts are sometimes called spathes, though they are quite different from anything in the Araceae.) Each spike bears staminate flowers. They are naked, devoid of perianth, almost always without bracteoles. Each staminate flower consists of a small or large aggregation of stamens, and there is a considerable variation of form; the stamens may seem to be separately and individually attached to the spike rachis, or be borne in small or large clusters on short or long axes (usually called columns or stemonophores). Pollen is often copious, but is dispersed quickly and also quickly ingested by the ubiquitous insect fauna of the inflorescences, which seems always and everywhere to include Nitidulid beetles and thrips, supplemented by roving, predatory earwigs. Pollen consumption is rapid and unless the collection is made early in anthesis and is quickly and adequately preserved, most of the pollen will be turned into frass and larvae. Numerous herbarium specimens of staminate collections now serve only to show floral form (if that), and lack pollen. Pollen characters are proving to be taxonomically useful, so care should be taken to preserve pollen in the specimens. If the collector has the facilities, liquid (FAA or just formalin) collections of staminate spikes should be obtained as supplementary to the dried material. The same is true of early stages of anthesis of female inflorescences.

The female inflorescences may also be simple or compound. If one applies this terminology to the gynoecial pattern of the flower, the same difference obtains. Consequently one may recognize four types of pistillate inflorescences; (a) with a single spike (head, or cephalium) formed of 1-carpellate flowers; (b) with several spikes formed of 1-carpellate flowers; (c) with a single spike formed of polycarpellate flowers; (d) with several spikes formed of polycarpellate flowers. In cases (a) and (c), the inflorescence is described as "solitary." This is the normal state in many, but not the majority, of *Pandanus* species, but is quite rare in *Freycinetia.* In cases (b) and (d), the inflorescence is "spicate" and this is the usual case in *Freycinetia,* and quite common in *Pandanus.* In *Sararanga,* as already mentioned, the massive inflorescence is always a richly-branched panicle.

In *Freycinetia,* the spikes (both male and female) tend to be closely adjacent and often ternate, so that the open ripe inflorescence seems to be an umbel. In a few cases (*F. angustifolia, F. jagorii*) the inflorescence is racemiform, as it is in nearly all species of *Pandanus* in the males, and in many species also in the females.

The bracts provide some useful characters, particularly as to color. On an inflorescence there is a spectrum of bracts, those at the base virtually leaflike, those subsequent each more altered, by the reduction of the length and the spread of the lower, colored part, until even the extreme apex is colored rather than green. The base is usually broadly expanded and boat-shaped, and the texture thinner or, especially in *Freycinetia,* actually thicker but much softer. In *Freycinetia,* the uppermost bracts are quite modified, becoming (in the apt phrase of Paul Cox) "solid bat nectar," i.e. soft, sugary, and entirely palatable. This does not occur in *Pandanus,* in which all bracts still retain a certain (if thin) stiffness. (The bract tex-

ture in *Sararanga* is unknown.) As the inflorescence ages, the bracts wither and many drop off or remain as tattered brown shreds and wisps. In *Freycinetia*, only a few basal bracts are retained and in ripening fruit these finally fall; most of the upper (visually, inner) bracts by this time have long since been eaten (around anthesis) or rotted away (later). But in *Pandanus*, the intermediate bracts usually wither and dry (turning brown) but remain in place on the ripening fruits; or, in the staminate inflorescence, dry up. The staminate rachis becomes fleshy and rots quickly, so that the inflorescence tends to break up as, or before, it falls. As already stated, this process is very rapid, taking only a few days, hastened by rapid chewing up of the softer parts by the local fauna of the inflorescence. In short, the collector usually only sees the full array of bracts in material at or before anthesis; and the colors are best, or only, visible then. The color, size, and details of the bracts afford a rather important means of correlating male and female of the same species; not that bracts of the two sexes are exactly alike, but they will be substantially similar. Naturally, collectors' observations on fauna, including possible pollen or seed vectors, will be of great value.

The fruits provide the most depended upon, readily observable, and preservable characters for identification. The components of the infructescence, besides the bracts and the rachises, are the heads (cephalia), or syncarps as they are sometimes called; this term however is rather ambiguous, as it can also be applied to the aggregate drupes, also termed polydrupes or phalanges, which are the main component units of the cephalium in those species which have them. In other species, with simple (1-celled) drupes, the term is not ambiguous but as it has been used for both cases, I prefer to abandon it and use the clearer term cephalium (or head). In any case, the cephalium, the drupe or phalange; and the details of each, provide numerous important taxonomic characters. It is almost essential, however, that the fruit be fully ripe. A great deal of confusion has been caused by unwary taxonomists unaware of relative states of maturity in dried specimens. This has led to "paper species" created on the basis of "false" characters, e.g. phalange dimensions. Unripe fruits also lack the critical mature coloration which can prove valuable taxonomically. On the other hand, well-preserved (particularly liquid-preserved) collections of young *flowering* pistillate material are highly desirable. However, when dried, this is sometimes so altered in aspect, lacking in useful marks, and in interior features, that it may be unidentifiable. Just as it is important to correlate male and female specimens, it is important to correlate fruiting with flowering pistillate collections.

In the drupes or phalanges, the style and stigma is of crucial importance taxonomically. In some species, these structures are either fragile (in many, they can be easily abraded or broken off), or they are severely altered by the drying process. In such cases close observation and sketches or sharp close-up photographs may preserve information later lost.

The leaves, apart from gross morphological data, provide a wealth of useful taxonomic information in their micromorphology. Data from anatomical and scanning electron microscope studies have shown that highly significant additional and correlative information can be extracted from a small sample of a leaf. However, this has to be based on a standardization. For such studies the sample must be: a segment of the leaf, about 1–3 cm long (i.e. along the leaf long axis), and including both margins, i.e. a complete median segment; or in large leaves or with minimal materials, a segment including one margin and the entire midrib, but omitting the other margin, will ordinarily suffice. This sample must be taken from a fully adult leaf, midway in the prophyll-leaf spectrum (i.e. representing the series of longest leaves). It must also be from an adult shoot (not a "sucker-shoot" or a flowering shoot with reduced leaves). And it must be from an adult plant, not a seedling or "sapling." In most cases, sufficient micromorphological data can be obtained from such segments removed from herbarium specimens, but it is more difficult in such cases to be sure that the standardization criteria have been met; hence, suitable leaves taken in the field might well be marked specially "*for anatomical study.*" (Anatomists using herbarium material would appreciate this.)

Separate pollen collections (preserved or thoroughly dried and disinfected) are highly desirable, as a great deal of pollen is lost through the usual drying techniques when making herbarium specimens.

Correctly labelled liquid-preserved specimens of heads or partial heads at anthesis are highly useful in the interpretation of stigmatic structure and this supplementary collecting is strongly

urged upon collectors who have the means available. (If FAA is lacking, strong alcohol or just formalin may suffice.)

Field Collecting Methods and Sampling

Small pandans of either *Pandanus* or *Freycinetia* can often be treated as any other plants, as whole branches with attached leaves, inflorescences or infructescences, and sometimes part of the root system, may be small enough to fit in standard size drying papers. Where inflorescences and infructescences are concerned, however, the advisability of providing supplementary liquid-preserved collections must be emphasized.

For bigger plants of any of the three genera, some careful sampling has to be done. Where the leafy stems are more than 2–3 cm in diameter, they can be split longitudinally. Such a method is helpful in reducing the thickness of specimens but has the disadvantage of cutting through the spiralled leaves in such a way that useful characters of the leaf-bases may be damaged or lost. Therefore, what is always required in such cases is the separate preservation of carefully detached leaves dried separately. They should be removed so that the whole sheath is intact (especially with auriculate *Freycinetias*); they can be folded back and forth, accordion-style, to fit into the drying papers. The tips of these leaves should be intact also; if they are naturally broken or abraded, each such leaf should be supplemented by a tip from another leaf so that the form, dentation, etc., of the complete apex is present. Unripe leaves from the center of leaf-crowns may provide such tips, but (because of basal growth) cannot provide adequate leaf-base and sheath or auricle characters. In *Freycinetia*, the auricles can best be sampled by carefully stripping away a series of leaves (older ones first) until the leaf-bases of leaves with fresh (i.e. not dried or withered) auricles are in view; these leaves should then be removed by circumferential shallow slicing, and preserved individually.

In *Pandanus* and *Sararanga* the adult leaf-bases are often very rigid and inconveniently large; they can be flattened readily if they are dried as separate halves (longitudinally divided). In species with very long leaves, leaf-length measurements can be supplemented by standard leaf segments; in such cases the segments have to be

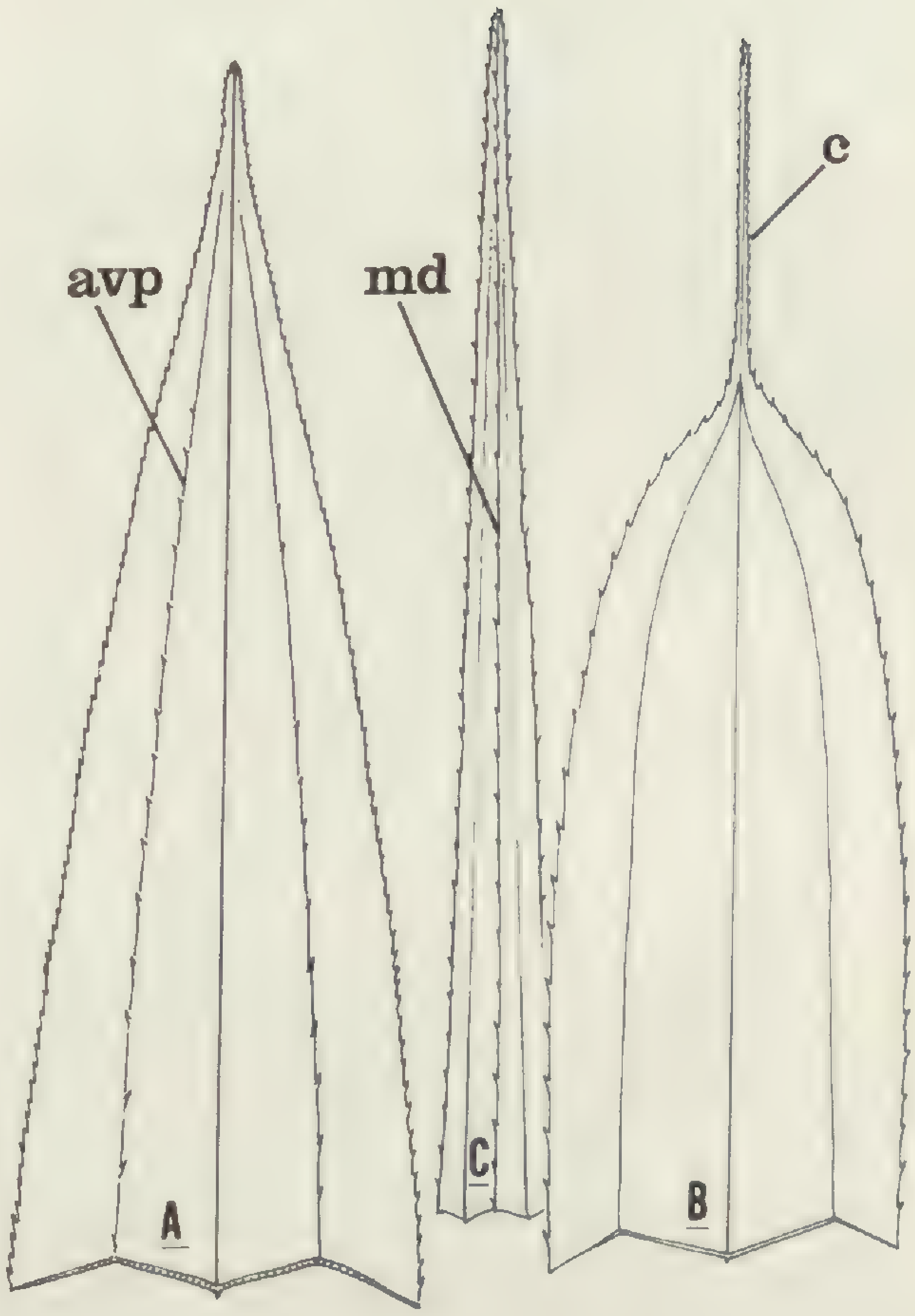

Figure 1. Types of leaf apices in Pandanaceae. A. Upper (ventral) surface of a species of *Pandanus* with denticulate apical-ventral pleats (avp). B. Upper (ventral) surface of a species of *Pandanus* (or *Freycinetia* or *Sararanga*) lacking denticulations on the apical-ventral pleats. C. Lower (dorsal) surface of a leaf apex showing the armed midrib. All the denticulations are antrorse.

numbered or lettered sequentially so they can be "reassembled" later for study. The collector has to make a pragmatic decision about how many leaves to collect; since each herbarium specimen may consist of one leaf, or less, and still be so bulky as to spill over onto two or more sheets, it is especially important that the collector provide careful and logical sampling techniques in the field. A choice of organs [prophyll, some scale leaves, some transitional bracts, fully-formed bracts, etc., as well as fully adult leaves, immature leaves, "sucker-shoot" leaves, and (when possible) seedlings] must be made so that a fuller knowledge of both leaf structural and dimensional variation, and age and developmental variation, is preserved inherently in the specimens. It cannot be overemphasized that such careful sampling techniques can be disrupted when duplicate specimens are sorted out and distributed; if at all possible, the bulk of the collection, or the most representative, should be re-

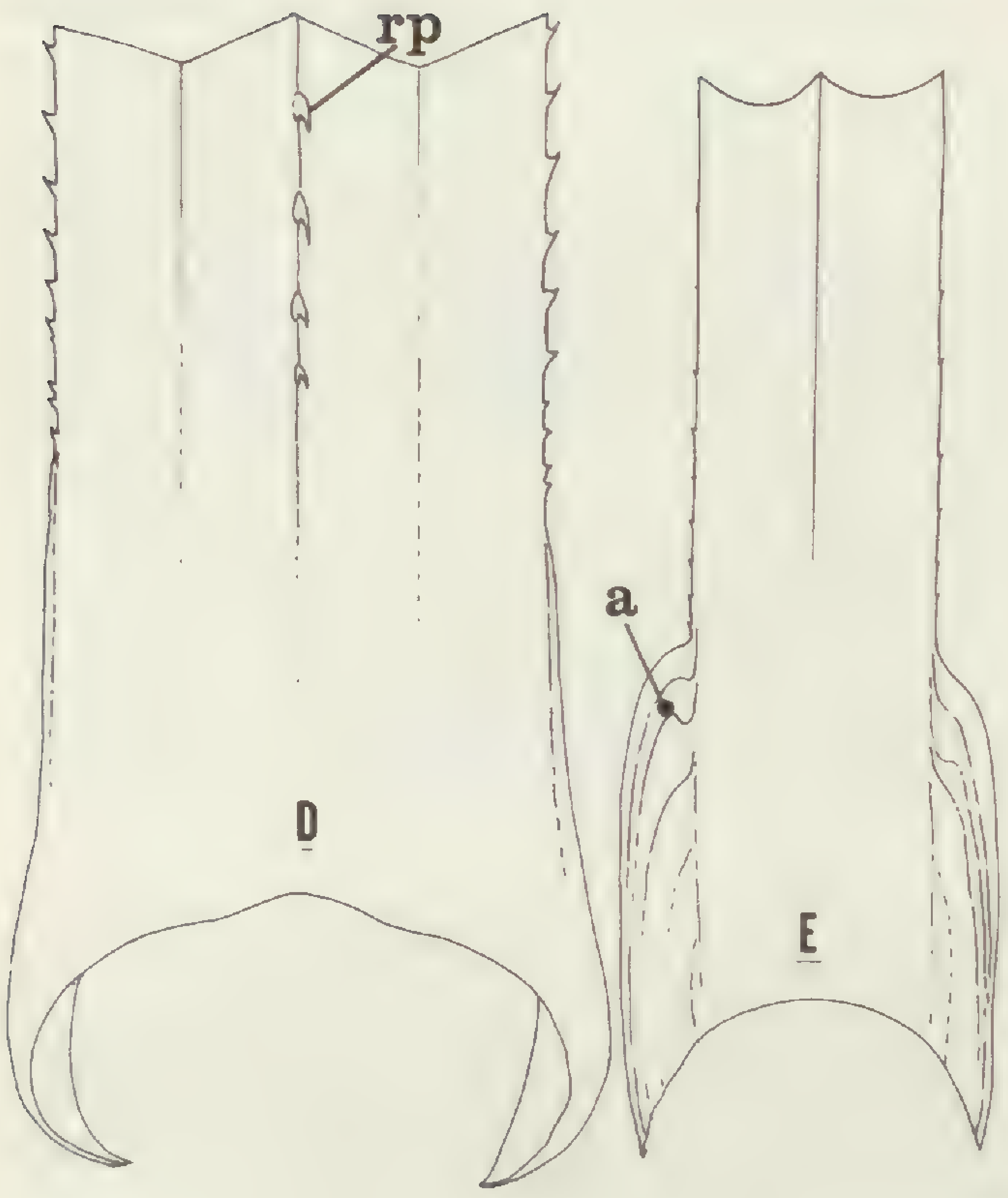

FIGURE 2. Types of leaf-bases in Pandanaceae. D. *Pandanus* and *Sararanga*. Leaf-base with no (or usually no) auricles; midrib near the base often (not always) armed with (often) recurved (retrorse) prickles. E. *Freycinetia*. Leaf-base with auricles (a), and unarmed basal portion of midrib.

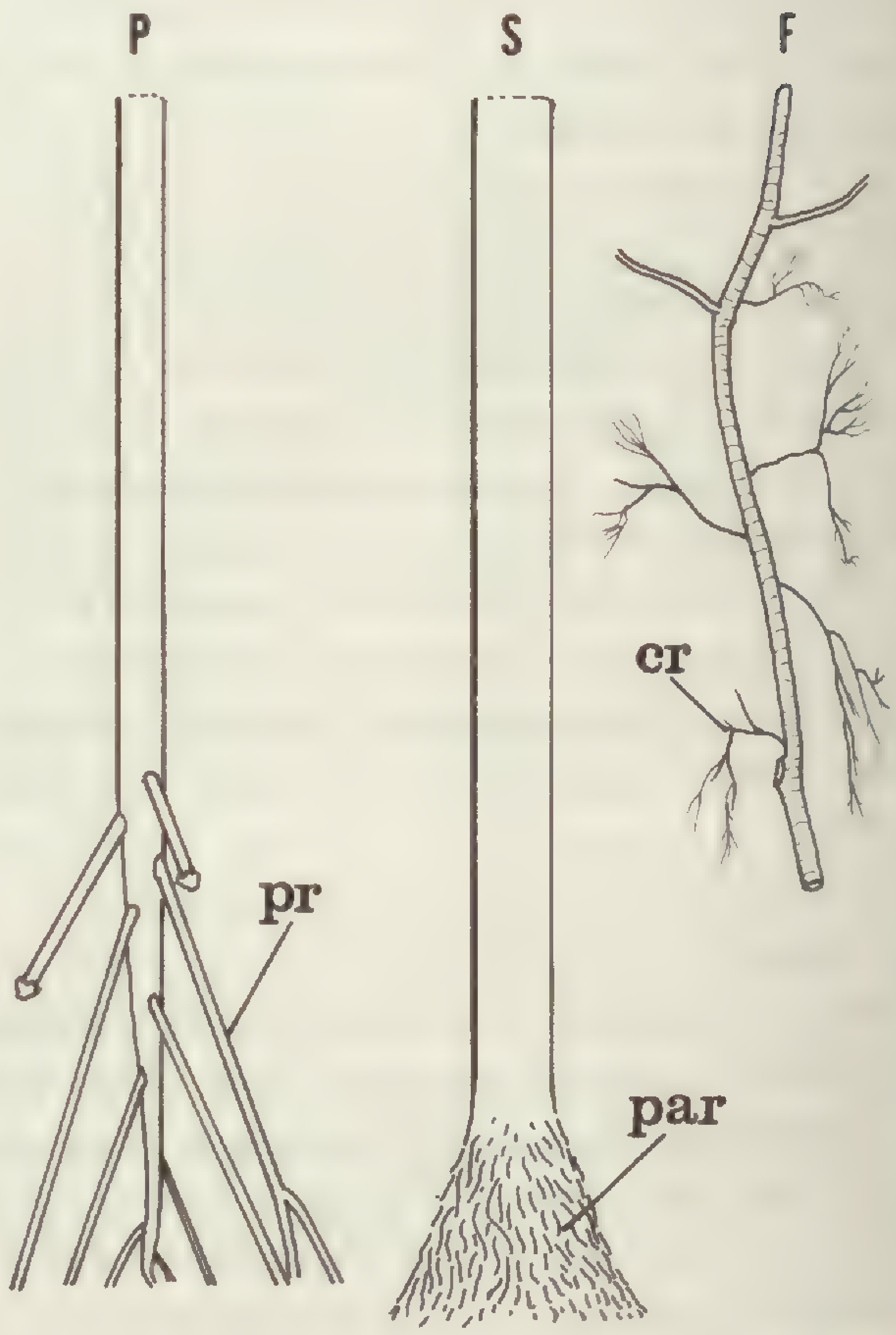

FIGURE 3. Habit in Pandanaceae. P = *Pandanus*: erect trunk, proproots (pr). S = *Sararanga*; erect trunk. palmoid roots at base (par). F = *Freycinetia*; climbing stem with clasping roots (cr).

tained until taxonomic study is completed. Duplicate specimens often appear which contain (for example) one prophyll, three phalanges, and a single leaf apex; needless to say, the form and the important diagnostic features of the plant cannot possibly be represented by such an aggregate of parts.

The goal of sampling should be to represent all possible organs and structures in such a way that a part, supplemented by notes, drawings, and photographs, can provide an accurate notion of the entirety. But this goal is more difficult when it comes to the whole habit of the plant, more so when variation in a population is found. However, thoughtful consideration of this problem usually results in some functional *ad hoc* technique that works fairly well. The question of *intra-population* variability is, at least in some species or complexes, a serious matter, which needs intensive study, in view of the sometimes drastic differences in taxonomic points of view expressed by different botanists concerned with the same species or species-groups. Thus, collection of a series of individuals (all, of course, carefully correlated and separately numbered) within a pragmatically determined population is a specific kind of collecting activity which is becoming urgent, particularly in such critical species as the *Pandanus tectorius* complex, the species of *Pandanus* sect. *Austrokeura*, the *Pandanus odoratissimus* complex, the *P. furcatus* complex, and certain groups of *Freycinetia*.

COLLECTING TOOLS AND EQUIPMENT

(1) A strong, sharp *parang* or *machete* or bush-knife; for very large specimens, a hatchet may also be useful.

(2) Pruning shears or sequiteurs.

(3) Thick gloves (pandans are always spiny and ready to attack).

(4) Field notebook.

(5) String tags (jewellers' tags). These are really necessary especially when leaves etc. are segmented sequentially. A small stapler is also helpful.

(6) Pencils and (preferably) India-ink pens: the latter are extremely useful for labels to be placed in liquid-preserved material.

(7) Plant presses—the usual materials.

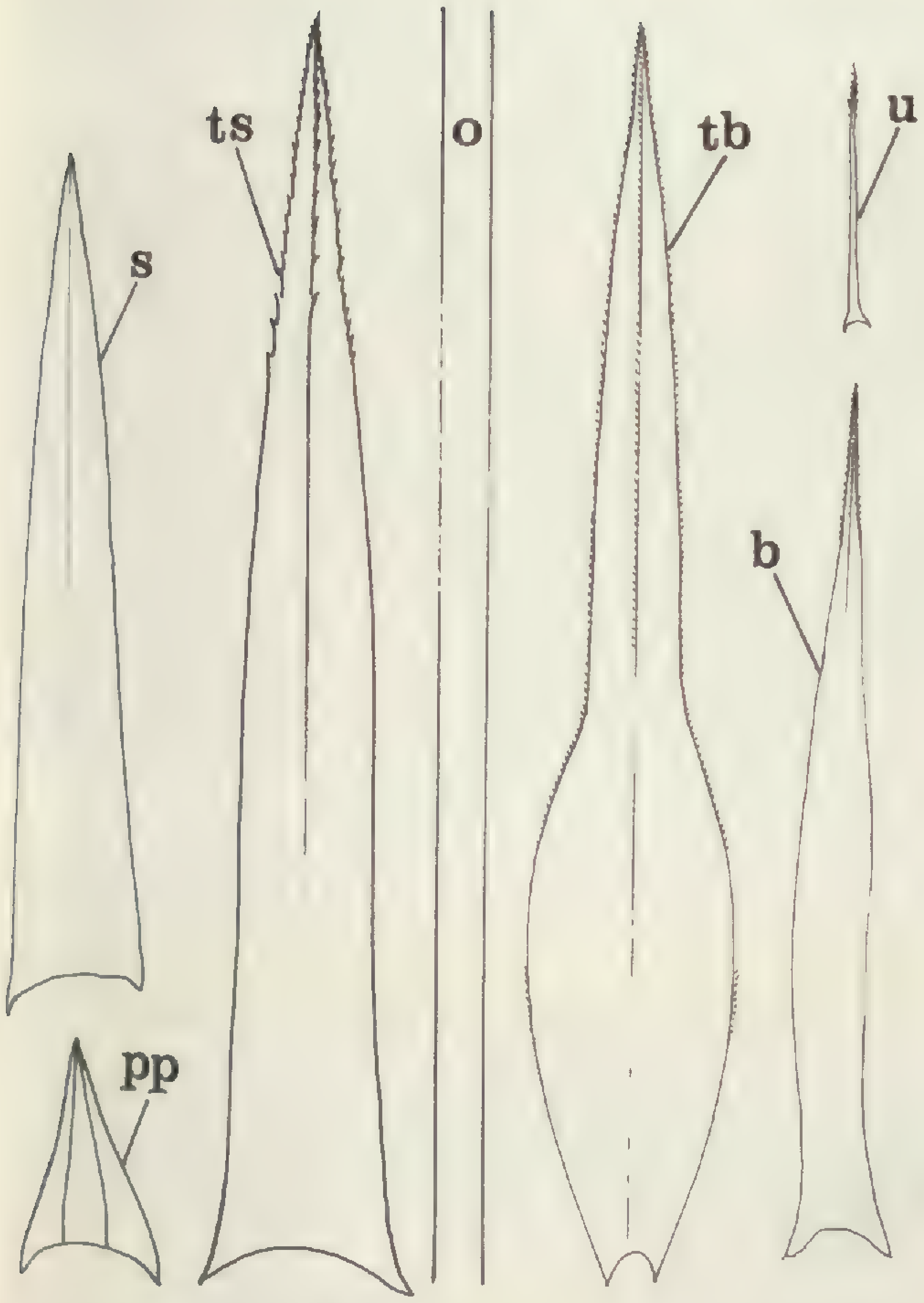

FIGURE 4. Leaf spectrum in Pandanaceae. Example drawn from a species of *Pandanus.* pp = prophyll (note twin costae). s = scale leaf. ts = transitional leaf (intermediate between scales and normal foliage). O = zone of normal foliage leaves. tb = transitional (inflorescence) bract; apex green and leaflike, base softer, expanded. b = normal bract, entirely colored. u = ultimate bract. Inflorescence terminates shoot meristem growth; branching occurs from next lower axil, the first organ to appear being the prophyll. Sequence repeats.

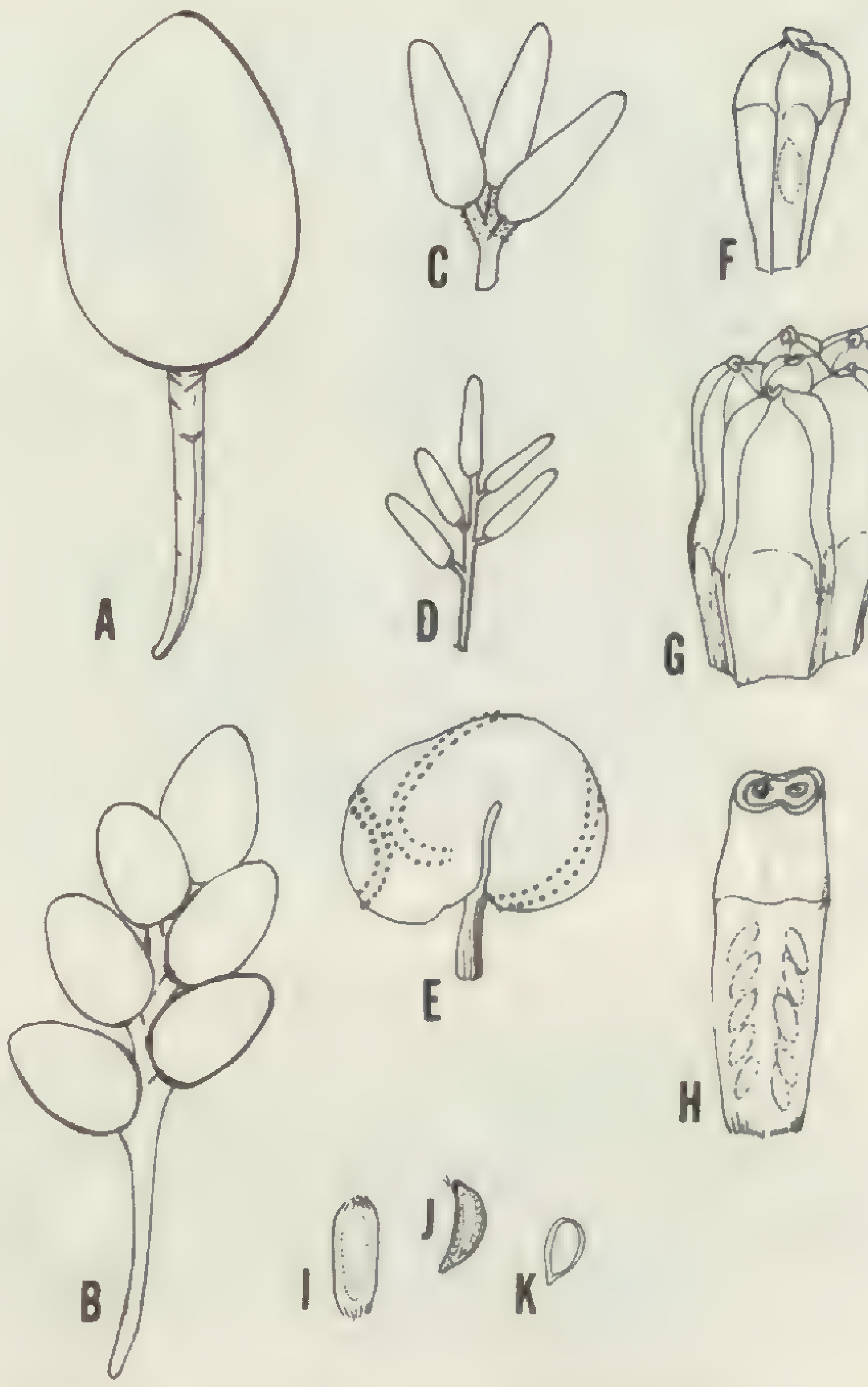

FIGURE 5. Types of inflorescence and fruit formation in Pandanaceae. A. Solitary cephalium. B. Spike of cephalia. C. Pseudumbel of (ternate) cephalia (*Freycinetia*). D. Raceme of cephalia (*Freycinetia*). E. Polyspermous berry of *Sararanga* (black dots are stigmas). F. Simple drupe of *Pandanus.* G. Polydrupe = phalange of *Pandanus.* H. Berry (bicarpellate, multiovulate) of *Freycinetia.* I. Pyrene of *Pandanus.* J. Seed of *Freycinetia.* K. Seed of *Sararanga.*

(8) Liquid preservative supply.

(9) Bottles and vials for liquid-preserved specimens.

(10) Powder-form fungicide (especially for pollen collections).

(11) Camera and film supply.

(12) Sketchbook (if additional to field notebook).

(13) Plastic bags.

(14) Cordage (string or nylon).

(15) Final labels.

LIVING COLLECTIONS

Pandans of almost any species are desirable for collection as ripe seed, small germinating seedlings, or cuttings. There are few botanic gardens with good collections of the family [among these may be mentioned first those tropical gardens that have outdoor collections, e.g. Bogor, Singapore, Kuala Lumpur, Lae, Peradeniya, Calcutta, Lucknow, Amani (? present status unknown), Fairchild, Tsimbazaza (Madagascar), Foster Garden and Pacific Tropical Botanic Garden, Hawaii, Sydney, Townsville, and Cairns; and those which have above average indoor collections, examples being Kew, Munich, and perhaps some others]. Even old established gardens tend to have very few species and frequently only one individual of a species (which, as they are unisexual, tends to be lost in due course). *Pandanus* seeds tend to be fairly long-lasting and, wrapped in moist sphagnum, can be airmailed almost anywhere and survive; germination tends to be a long affair. *Freycinetia* seeds tend to germinate more rapidly; little is known of their horticultural requirements. Except for the Lae Botanic Gardens, the genus *Sararanga* is (I think) quite unknown in cultivation; further distribu-

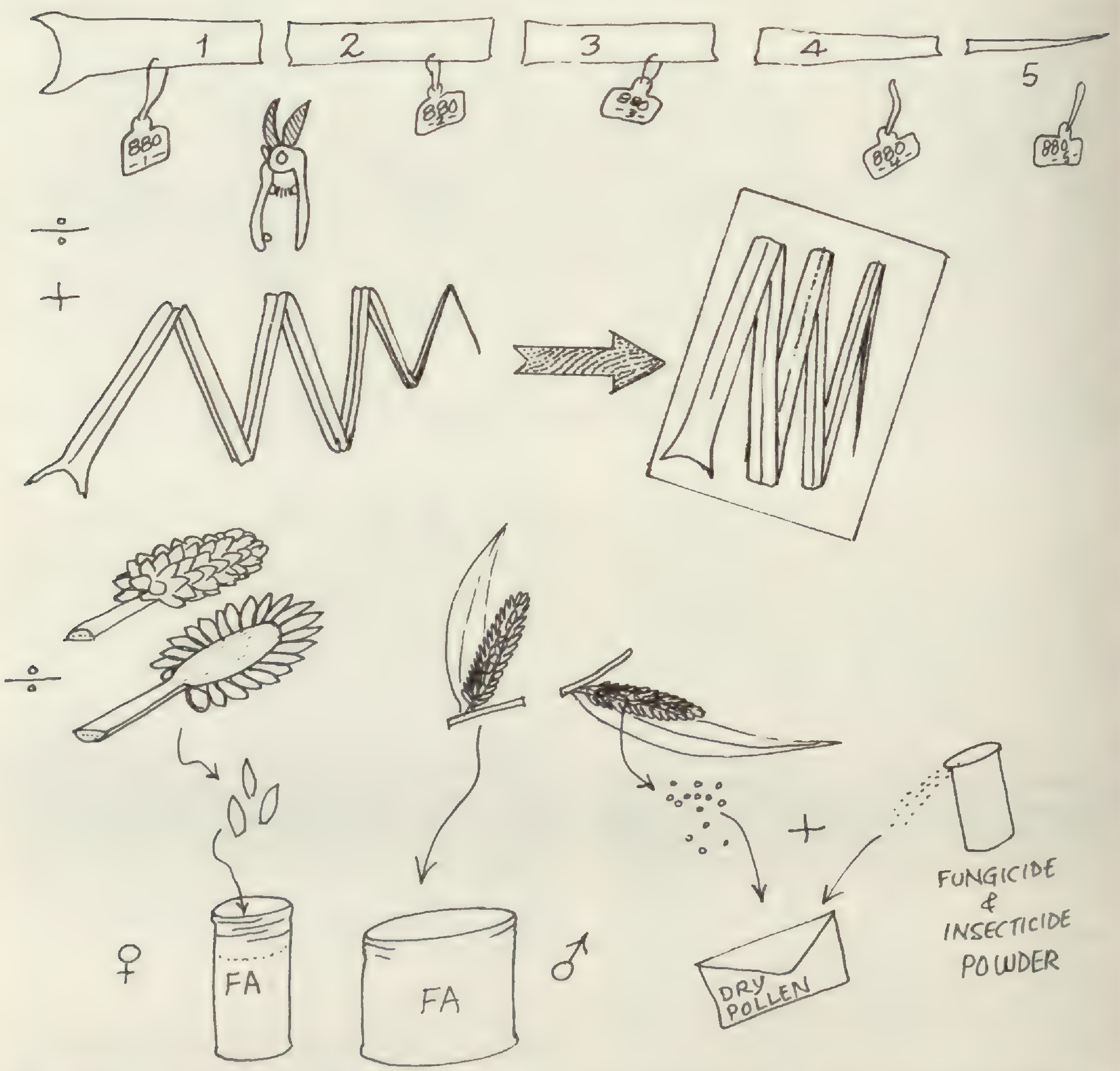

FIGURE 6. Some suggestions for collecting specimens of Pandanaceae. Above: large leaf, segmented, the segments numbered sequentially with both the collector's number and the leaf-segment number. Below this, a leaf folded back and forth *à la* accordion pleats to fit on the herbarium sheet. Below: fruit longitudinally divided and some of the phalanges or drupes preserved; staminate spike similarly divided, parts also preserved; pollen preserved in envelope with insecticide and fungicide powders. All treatments sequential to photography and note-taking.

tion, specifically of *S. philippinensis*, and of both sexes of both species, is highly desirable. The pandans in general tend to be horticulturally interesting and often curious or unusually elegant, and tend to cause considerable public interest. The species that are already comparatively well known in cultivation are few and can be conveniently listed here so collectors can (if they wish) avoid the slightly more elaborate task of collecting and distributing living material for propagation: *Pandanus tectorius*, *P. odoratissimus*, and most of the "horticultural" varieties of both of these (especially the striped, variegated leaf forms); *P. utilis*; *P. pygmaeus*; and *P. dubius* (known in horticulture as "*P. pacificus*"). The only freycinetias in cultivation tend to be *F. funicularis*, *F. multiflora* (of *F. cumingiana*), and *F. sumatrana*, and even these tend to be restricted to tropical gardens; nearly any *Freycinetia* is worth introducing to a botanic garden.

Environmental requirements for most species can only be deduced from natural habitat conditions, so the seed distribution should always include useful notes on these. Many pandan

species are rather indifferent to a number of parameters, but others tend to be very finicky. Critical factors tend to be soil pH and soil moisture retention (swamp pandans tend, as might be expected, to be ecologically very narrow-minded, while savanna species are pretty tolerant). Atmospheric humidity and nocturnal temperature regimes may also be very important. So little is known in detail, however, that most attempts will have to be regarded as experimental, particularly in habitats fairly unlike the origin. Palm species tend to be fairly good comparisons; if a pandan from the same region and basic habitat as an existing palm species in cultivation is grown under the same conditions as the palm, there is probably a good chance of succeeding with the pandan as well.

Identification of Pandanaceae

Apart from a few major herbaria, advice and identifications can usually be obtained from the fairly small number of specialists on the family, of whom (I believe) I can append the following virtually complete list: the author (B. C. Stone, Herbarium, Botany Dept., University of Malaya, Kuala Lumpur 22-11, Malaysia); Dr. H. St. John, B. P. Bishop Museum, Honolulu, Hawaii; Mr. Robert Tucker, Anderson Botanic Gardens, Townsville, Queensland, Australia (especially for Australian species); Dr. K.-L. Huynh, Institute Botanique, Université de Neuchatel, Switzerland (particularly for determinations based on sterile or staminate collections of unknown correlation, through microtechnical methods).

Personally I am always ready to receive and identify specimens of Pandanaceae from any part of the world.

Guide to the Illustrated Section

A number of sketches are attached with the idea of familiarizing the reader with the basic parts of pandans, some of their gross variability, and some special collecting techniques.

STUDIES ON THE REPRODUCTIVE SYSTEM OF *NIVENIA CORYMBOSA* (IRIDACEAE), AN APPARENTLY ANDRODIOECIOUS SPECIES[1]

ROBERT ORNDUFF[2]

ABSTRACT

Nivenia corymbosa has flowers with a stamen- and style-length dimorphism but pollen monomorphism. Results of an intra- and intermorph crossing program suggest that this species is androdioecious rather than conventionally distylous. A single progeny grown from a selfed long-styled plant contained 1 : 1 longs : shorts, suggesting that the longs of the ancestral distylous condition are the heterozygous morph rather than the homozygous one.

The small South African genus *Nivenia* is of interest because it is one of two genera of Iridaceae in which heterostyly has been reported (Ornduff, 1974).[3] Three species of this small woody genus are reportedly distylous with one morph having an exserted style and short stamens, and the other having exserted stamens and a short style. In *N. binata* Klatt, distyly is associated with pollen dimorphism as well (Mulcahy, 1965). At least three species of *Nivenia* are monomorphic with a floral morphology resembling that of the long-styled form of the distylous species (Ornduff, 1974). This paper presents the results of an artificial pollination program using the dimorphic *N. corymbosa* (Ker) Baker that was designed to determine the presence and nature of incompatibility in this species.

MATERIALS AND METHODS

The crossing program utilized four field-collected short-styled plants of *N. corymbosa* and one short- and four long-styled plants derived by selfing a long-styled plant. The terms "long" and "short" will be used in this paper to refer to these two morphs, but in view of the apparent androdioecism of this species, they are not equivalent to the usage of "pin" and "thrum" of distylous species. The material orginated from Bains Kloof, Cape Province, South Africa (*Ornduff 7666*, UC). Plants were grown in an insect-free greenhouse in Berkeley and pollinations were made using fine-tipped forceps. Self-, intramorph, and intermorph pollinations were carried out, and as controls some flowers were left unpollinated and others were emasculated. One long-styled plant was selfed and the style length of the progeny scored. As capsules matured, they were placed in seed packets and the number of seeds was counted at the end of the program. Pollen viability, size, and wall sculpturing were determined using pollen grains from two plants of each morph mounted in aniline blue-lactophenol or lactophenol.

RESULTS

The pollen viabilities of the field-collected plants ranged from 92 to 100 percent and of the progeny grown from seed from 56 to 95 percent. Pollen size was monomorphic: for two longs $\bar{X}$ 37.7 μm ($\sigma = 1.8$) and 37.3 μm ($\sigma = 2.2$) and for two shorts $\bar{X}$ 37.7 μm ($\sigma = 1.8$) and 41.4 μm ($\sigma = 2.1$). Wall sculpturing was also monomorphic.

None of the emasculated or intact control flowers produced seeds (Table 1). Self-pollinations of shorts produced no seeds and of longs produced an average of 0.04 seeds per pollination. Intramorph pollinations of shorts and longs produced an average of 0.2 seeds per pollination. Intermorph pollinations of shorts as seed parents produced an average of 0.3 seeds per pollination and of longs as seed parents 3.4 seeds per pollination. The single progeny grown from a selfed long contained 6 longs and 6 shorts.

DISCUSSION

The presence of an incompatibility system in *Nivenia corymbosa* is evidenced by the lower seed set following intramorph pollinations compared

[1] Supported in part by grants from the National Science Foundation and the Committee on Research, University of California, Berkeley.

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[3] The other genus for which heterostyly has been reported is *Geissorhiza*, in which plants of some populations of *G. heterostyla* L. Bolus have dimorphic flowers that are not conventionally distylous (Ornduff, 1974).

TABLE 1. Results of intramorph and intermorph pollinations of *Nivenia corymbosa*.

Cross[1]	Number Flowers Utilized	Number Capsules Produced	Number Seeds Produced	Number Seeds per Pollination
Controls:				
SP1 (intact, unpoll.)	11	0	0	0
LP2 (intact, unpoll.)	21	0	0	0
LP2 (emasc., unpoll.)	18	0	0	0
LP3 (intact, unpoll.)	16	0	0	0
Self-pollinations:				
SF1	49	0	0	0
SF2	69	0	0	0
SF3	92	0	0	0
SF4	56	0	0	0
LP2	52	1	3	0.06
LP4	15	0	0	0
Intramorph cross-pollinations:				
SF1 × SF2	14	5	26	1.9
× SF3	23	0	0	0
SF2 × SF3	26	0	0	0
SF4 × SP1	55	5	5	0.09
SP1 × SF4	28	5	2	0.07
LP3 × LP2	53	3	9	0.2
Intermorph pollinations:				
SF4 × LP2	59	8	22	0.37
SP1 ×LP2	29	4	3	0.1
LP1 × SF4	56	21	230	4.1
LP2 × SF1	1	1	4	4.0
× SF4	41	20	115	2.8
LP3 × SF4	31	12	87	2.8

[1] Code numbers of individual plants are used: F = field-collected plant, P = progeny of selfed field-collected plant; L = long, S = short.

with that following intermorph pollinations of pins. However, the average seed production of shorts following intermorph pollinations is approximately equal to that following intramorph pollinations and does not exceed 5 percent of the average maximum seed set of longs. The pollen viability of one short used as a seed parent in an intermorph cross was reduced (69 percent) but in the other individual it was high (97 percent), so the low fecundity of these crosses probably should not be attributed to gametic sterility factors. It is also possible that this difference in seed set between the two morphs is attributable to mechanical problems in depositing sufficient pollen grains on short stigmas. This does not seem to be a likely explanation for these differences, since observations of pollen loads on naturally-pollinated stigmas of *N. binata* (a species with a floral morphology very similar to that of *N. corymbosa*) collected at Swartberg Pass, Cape Province, indicated an average number of 33.3 pollen grains on long stigmas and 27.8 pollen grains on short stigmas (with no attempt to discriminate visually between intra- and intermorph pollen grains; Ornduff, pers. obs.). If such figures are a measure of normal stigmatic pollen loads carried by fecund individuals of the distylous *N. binata* in the field, the number of compatible pollen grains per stigma required for modal seed set of both longs and shorts is very low and would likely be deposited on stigmas via artificial pollinations. A third possible explanation of the observed seed set in *N. corymbosa* is that the species is essentially androdioecious, that is, some individuals produce perfect flowers and others produce staminate flowers. The data at hand, including the occurrence of pollen monomorphism in this species, are compatible with this suggestion. That some shorts occasionally produce small numbers of seeds suggests that androdioecism is not fully developed in this species.

Various types of reproductive systems involving a sexual separation have evolved from heterostyly in other groups. These include full dioecism in some members of the Rubiaceae and Menyanthaceae and androdioecism in *Oxalis suksdorfii* (see Ganders, 1979). That various modifications of the distylous breeding system have evolved elsewhere in *Nivenia* is evidenced by the occurrence of long-styled monomorphism in at least three species with apparent associated self-compatibility in *N. stokoei* (Guthrie) N. E. Brown (Ornduff, 1974). The 2:1 rather than 1:1 long : short morph ratio of a field population of the distylous *N. binata* also suggests that the breeding system of this species may deviate from that expected for a conventional distylous species (Ornduff, 1974).

It is of interest to note that the progeny of a selfed long-styled plant of *Nivenia corymbosa* produced a 1:1 ratio of longs to shorts. Assuming that the androdioecism of this species is derived from a more conventional distylous ancestral condition, this suggests the possibility that in *Nivenia* longs are the heterozygous genotype, a

condition otherwise known for certain in the distylous *Hypericum aegypticum* (Ornduff, 1979) and also possibly in the dimorphic *Armeria maritima* (Baker, 1966). For those interested in the comparative evolution of breeding systems and in the selective forces that lead to the breakdown of heterostyly, *Nivenia* clearly merits further attention and field studies are particularly needed.

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A TAXONOMIC REVISION OF *CONDYLOCARPON* (APOCYNACEAE)[1]

MARY E. FALLEN[2]

ABSTRACT

Condylocarpon, which has a center of distribution in Brazil and the Guianas, has been infrequently collected and thus is not well known. Here the number of species is reduced from 17 to 7, and the new combination **Condylocarpon intermedium** Muell.-Arg. subsp. **laxum** (Muell.-Arg.) Fallen is made. Peculiar petal appendages, fruit type, and the shape of the style-head are shown to be important taxonomic characters that can be used to define two basic groups within the genus.

Condylocarpon is a small neotropical genus of Apocynaceae occurring in disjunct habitats from Nicaragua to Brazil. Five of the species are endemic to Amazonian Brazil, the Guianas, and adjacent regions, suggesting an Amazonian origin for the genus. Although some of the species are geographically wide-ranging, all tend to be ecologically restricted to special life zones. Most are members of the lowland wet or moist forest community. One occurs in the more xeric cerrado community; another, the only species of *Condylocarpon* to occur outside continental South America, has fruits that show adaptations for salt water dispersal, and therefore occurs also in coastal habitats. All species are woody forest lianas with small, inconspicuous flowers and dry, indehiscent fruits. *Condylocarpon* is found mostly in lowland forest. According to label information for the specimens that I have seen, more than 80 percent were growing along river banks. Although this may be an artifact of the intensive collecting along rivers that are important transportation routes, it suggests that these indehiscent fruits may be broken apart and dispersed by water. Trends of diversification are illustrated by elaboration of the corolla lobes and modifications of the articulated fruit. Due to their narrow ecological habitats, most species have been collected only rarely. The last comprehensive treatment was by Mueller-Argoviensis (1860), who recognized 11 species. Six of these species are maintained here and one is treated as a subspecies. Of the six species that have been described since 1860, five are reduced to synonymy.

TAXONOMIC HISTORY

Condylocarpon was validly published by Desfontaines (1822), who described the species *C. guyanense* based on a fruiting specimen sent to him by Joseph Martin, director of the Jardin de Botanique de Cayenne, French Guiana. The description is quite accurate with the exception of his interpretation of the areolate tertiary venation on the lower leaf surface as groups of scales.

In the *Prodromus*, DeCandolle (1844) recognized two species of *Condylocarpon*. In addition to *C. guyanense*, he correctly assigned *Echites isthmica* (Vellozo, 1829) to *Condylocarpon* and made the new combination. He also described *Maycockia*, honoring Dr. James Maycock, a physician and naturalist, who in the early part of the 19th century compiled a catalogue of the plants in Barbados. The type of the new genus, *M. rauwolfiae*, is synonymous with *Condylocarpon isthmicum*. Because Vellozo's type specimens were lost, the type for *Condylocarpon isthmicum* is the plate of *Echites isthmica*, which appeared in Vellozo's (1829) *Flora Fluminensis*, the poor quality of which was noted by DeCandolle (1844) in the new combination, as well as by Mueller-Argoviensis in his later treatment of the group in Martius' *Flora Brasiliensis* (1860). Although the plate of *Echites isthmica* includes flowers as well as fruits, the flowers are so ambiguously depicted that little more can be discerned than that the corolla is 5-parted. The type, therefore, must be considered functionally as a fruiting specimen. Thus at the time DeCandolle described the genus *Maycockia*, the only two species known to belong to the genus *Condylo-*

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carpon—*C. guyanense* and *C. isthmicum*—were known only from fruiting specimens. Since the type of *Maycockia* was based on a flowering specimen, it is understandable that DeCandolle failed to recognize the two genera as synonymous.

In 1851, Miquel published the description of an apocynaceous liana collected in Suriname as the type of a new genus. He noted that it was a peculiar genus showing affinities to *Tabernaemontana* and *Ochrosia* and he named it after Nicolas Hortsman, an early explorer in the Guianas and Pará, Brazil. *Hortsmania* is synonymous with *Condylocarpon*. It is possible that Miquel failed to recognize this specimen as belonging to the genus *Condylocarpon* due to the unusual fruit development of this species, in which only one of the paired carpels develops, with only the lowermost seed in that carpel maturing, so that instead of the usual paired, multiarticulate fruits, which are characteristic for most species in the genus, *C. myrtifolium* has a solitary, single-seeded fruit.

Mueller-Argoviensis' monograph of the genus (1860) appeared in his treatment of the Apocynaceae in Martius' *Flora Brasiliensis*. He was the first to connect *Maycockia* and *Hortsmania* with *Condylocarpon* and make the reassignments. In addition he described seven new species from specimens collected in Brazil by such well-known collectors as Schott, Riedel, Spruce, and Sellow.

Rhipidia is also synonymous with *Condylocarpon*. Described by Markgraf in 1926 from a fruiting specimen collected in Pará, as *Anechites* (?) *amazonica*, it was raised by him to generic rank when he received flowering material in 1930. Markgraf realized that there was a close affinity between *Rhipidia* and *Condylocarpon*, but he recognized the former as distinct on the basis of its short corolla lobes, high placement of the stamens on the corolla tube, ovarian disc, and hairy, filiform fruit. *Rhipidia* was reduced to synonymy under *Condylocarpon* by Ducke (1943), who at that time described two new Amazonian species of *Condylocarpon*, *C. hirtellum* (= *C. pubiflorum*) and *C. reticulatum* (= *C. amazonicum*).

GENERIC RELATIONSHIPS

There is, unfortunately, no standard intrafamilial classification system for the Apocynaceae. Schumann's treatment of the family in Engler and Prantl's "Die natürlichen Pflanzenfamilien" (1897), and the studies put forward in a number of papers by Pichon (1948a, 1948b, 1951) are the most recent comprehensive studies of the family.

Condylocarpon is a member of the large, heterogeneous subfamily Plumerioideae by virtue of its completely fertile, basally unappendaged anthers, which are not adherent to the style-head. Following Schumann, the apocarpous, bifid fruit of *Condylocarpon* put it in the tribe Plumerieae. He splits the Plumerieae into four subtribes: Alstoniinae, Tabernaemontaninae, Rauwolfiinae, and Cerberinae, based, in part, on number of seeds per carpel.

Segregation based on 2, 4, or 6 seeds per carpel (Rauwolfiinae and Cerberinae) versus many seeds per carpel (Alstoniinae and Tabernaemontaninae) is problematic. Markgraf (1930) criticized Schumann's placement of the "typically few-seeded" *Condylocarpon* in the Alstoniinae. He felt that *Rhipidia* (= *C. amazonicum*) showed affinity to *Anechites* by the ovarian disc and the structure of the fruit, and that these two genera, together with *Condylocarpon*, formed a natural group within the Rauwolfiinae. However, *Condylocarpon* shows a fourfold variation in the number of ovules per carpel. Therefore, Schumann's system is not useful for the classification of *Condylocarpon* beyond tribal rank.

In his classification of the Plumerioideae, Pichon (1948b) split the subfamily into seven tribes, based, for the most part, on whether the fruits were dehiscent or indehiscent, and dry or fleshy. He maintained *Rhipidia* and *Condylocarpon* as separate genera within his tribe Rauvolfiae, due to differences of the "disc" of *Rhipidia*, and in their fruit structure (apparently not having seen Ducke's (1943) publication). Together these two genera comprise his subtribe Condylocarpinae, which he notes as having problematic affinities.

I agree with Pichon that *Condylocarpon* is a member of the Rauvolfieae. However, I do not support his system beyond tribal rank. His subtribes are often too narrowly circumscribed and suggest insufficient study. I feel that it is premature at this time to assign subtribes within the Rauvolfieae. A more in-depth study of the taxa involved is necessary in order to recognize and evaluate phylogenetic relationships within the tribe. I disagree with Markgraf (1930) that *Condylocarpon* and *Anechites* are closely related. My studies of *Condylocarpon* have failed to reveal the disc that he describes. In *Anechites*, on the other hand, the disc is well-developed and distinct from the ovary. The resemblance of the

fruits of *Condylocarpon amazonicum* to those of *Anechites* is probably best explained by convergence. Both genera are forest lianas with indehiscent fruits, and it is logical that a light, one-seeded mericarp covered with hairs has evolved independently in both genera as an aid to dispersal.

The structure and differentiation of the style-head is an extremely valuable taxonomic character in the Apocynaceae (Schick, 1980; Fallen, 1983). The style-head has, for the most part, been relatively little affected by habitat conditions, and, together with the structure of the anthers, it provides one of the most reliable means of recognizing natural groupings of taxa. The style-head of *Condylocarpon* is unusually simple and undifferentiated. This type of style-head, the indehiscent fruits, and the longitudinally folded seeds suggests a close relationship with *Alyxia*, a paleotropical genus of about 120 species, and to a somewhat lesser extent, with the pantropical genus *Rauvolfia*.

Morphology

Leaves

Of the seven species of *Condylocarpon* recognized in this treatment, two (*C. guyanense* and *C. isthmicum*) have three leaves per node; the other species all have opposite leaves. With the exception of *C. myrtifolium*, which has extremely consistent leaf characteristics, the leaves tend to show considerable variability within a species in both their size and shape. The leaves of all species are entire and glabrous to subglabrous adaxially. The abaxial surface is glabrous in *C. glabrum*, *C. guyanense*, and *C. myrtifolium*, and pilose only along the midvein in *C. intermedium*. The nature of the adaxial surface in the other three species shows a wide range of interspecific variability. Therefore, leaf characteristics seem to be of relatively little taxonomic value, although they have frequently been employed in specific and particularly supraspecific delimitations in earlier treatments. The more adequate herbarium material now available provides a better perspective of the range of variability within the genus.

Inflorescence

The inflorescence in *Condylocarpon* is a many-flowered thyrse. These thyrses may be terminal only or terminal and axillary. They often exhibit a congested growth that makes them appear cyme- or even umbellike (Fig. 1).

Flowers

The calyx of *Condylocarpon* is regular, pentamerous, and without squamellae on the adaxial surface of the sepals.

Aestivation is sinistrorse and the corolla is globose in bud in most species. The latter aspect may be partly due to the bulk of the inwardly rolled appendages of the corolla lobes. Although the corollas of all species are less than 1 cm in diameter, they exhibit variety in form as well as in relative size. A very useful character for specific delimitations within the genus is the structure of the corolla lobes. In some species (i.e., *C. glabrum*, *C. guyanense*, *C. intermedium*, and *C. isthmicum*) the corolla lobes are equipped with lorate appendages that are speckled or streaked with reddish brown to red-violet markings on the abaxial surface. The corollas of these species may be up to 7 mm across, but greater than half of this distance is accounted for by the appendages themselves; the diameter without the appendages is no more than 2.0–2.5 mm (Fig. 2A). The corolla lobes of the other species lack lorate appendages. In *C. myrtifolium* they are shortly auriculate and ascending. This is the smallest-flowered species, with corollas about 3.5 mm in diameter, including their short, acuminate petal tips (Fig. 2B). The corolla lobes of *C. amazonicum* and *C. pubiflorum* are oblique and spreading to slightly ascending. The corollas of *C. pubiflorum*, 9 mm in diameter, are the largest in the genus (Fig. 2C).

The stamens of *Condylocarpon* have filaments about 0.2 mm long and are inserted midway or slightly above in the corolla tube. The anthers are ovate to lanceolate and range from 0.3 to 0.5 mm in length. The thecae are fertile completely to the base. The anthers are without sterile basal appendages and are not adherent to the style-head.

The style-head of *Condylocarpon* is one of the least specialized that occurs within the Apocynaceae. It is orbicular in most species (Fig. 2D), but turbinate in *C. amazonicum* and *C. pubiflorum* (Fig. 2E), and has two free apical appendages. It is covered with secretory papillae and shows no regional differentiation of the epidermal cells (Fig. 3). The style elongates very little during development, so that at anthesis the style-head is subsessile or with a style no more than

FIGURE 1. *Condylocarpon guyanense.*

0.4 mm long. The gynoecium is apocarpous, being composed of two carpels that are united at their apices by the common style-head. The ovary is conical, glabrous, and ranges from 0.3 to 0.8 mm in height.

Condylocarpon has usually been described as lacking nectaries or a disc (Miquel, 1851; Mueller-Argoviensis, 1860; Miers, 1878). However, Markgraf (1930) described *Rhipidia* (= *Condylocarpon amazonicum*) as having a disc, and used

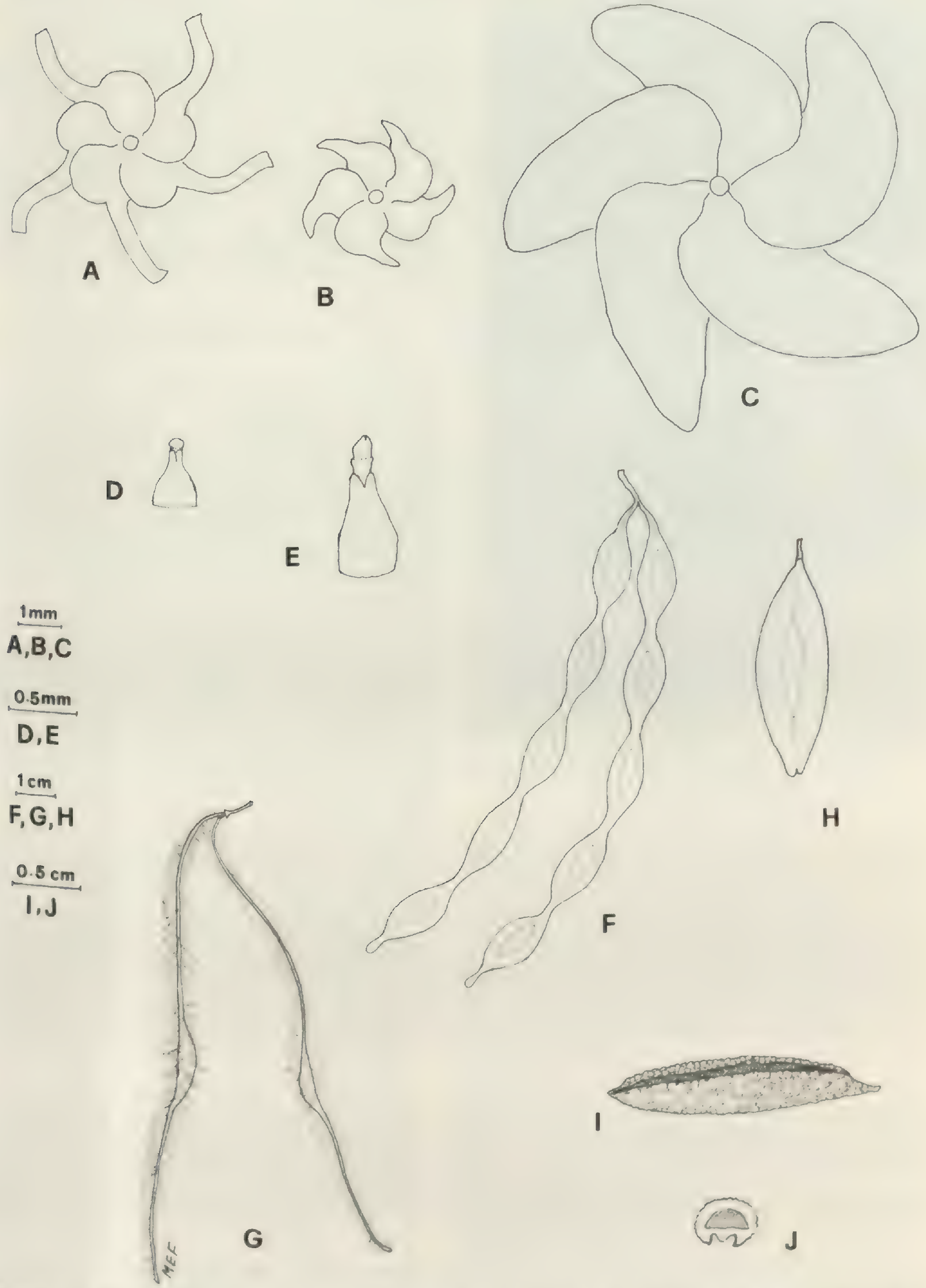

FIGURE 2. Basic structural types of *Condylocarpon*. A–C, corolla: A, *C. isthmicum*; B, *C. myrtifolium*; C, *C. pubiflorum*. D–E, style-head: D, *C. guyanense*; E, *C. amazonicum*. F–H, fruit: F, *C. isthmicum*; G, *C. amazonicum*; H, *C. myrtifolium*. I–J, seed, *C. pubiflorum*: I, from the side; J, in transverse section.

FIGURE 3. Scanning electron micrograph of the gynoecium of *Condylocarpon guyanense.*

this as one of the criteria to distinguish *Rhipidia* from *Condylocarpon.* Ducke's (1943) description of *C. reticulatum* included a disc. He stated at the end of the description that the study of the ovary of dried material was very difficult, and that the data used in the diagnosis were provided by Dr. Kuhlmann. I have studied the gynoecia of all species in serial sections and have found no distinct disc. Nectar seems to be secreted from the ovary wall. Markgraf's and Ducke's mistake may be due to the lobed appearance of the ovary base in desiccated material.

The number of ovules per carpel is usually four, with the ovules arranged biserially (*C. amazonicum, C. glabrum, C. guyanense,* and *C. myrtifolium*). In both *C. amazonicum* and *C. myrtifolium* all but one of the ovules in each carpel degenerate during development, resulting in a single-seeded carpel at maturity. In *C. myrtifolium* one of the carpels degenerates as well. Both *C. intermedium* and *C. isthmicum* usually have five or six ovules per carpel, and the specimens that I have examined usually had four or five seeds in each mature carpel. The ovules of *C. pubiflorum* are arranged in four or five rows rather than biserially, and have a greater number of ovules per row than in the other species, so that the usual number of ovules per carpel is ca. sixteen. Only three of the fifteen fruiting specimens of *C. pubiflorum* that were available to me for study had intact, mature fruits. These had 12, 15, and 16 developed seeds per carpel, respectively; I surmise that most of the ovules in this species usually reach maturity.

Fruit

The fruit of *Condylocarpon* is usually composed of two pendulous, woody, indehiscent mericarps. In those species that have lorate corolla appendages, the mericarps are glabrous and articulated into several one-seeded, somewhat flattened or angled segments (Fig. 2F). In *C. guyanense* and *C. isthmicum* the carpels are flattened. The seed-containing segments are broader than the sterile regions between them. The tissue of the ovary wall at maturity contains many air spaces, making the fruits lightweight and buoyant. Fruits of *C. isthmicum* remained afloat in the lab for 16 days. The segments of *C. intermedium* are 3-angled in transverse section, and at maturity the seed-containing segments are inflated, the inner ovary wall being composed of a light, corky tissue about 3–4 mm thick. In the regions linking the seed-containing segments the carpel is only a few millimeters in diameter and lacks a corky layer. The breaking up of the carpel at the constrictions would result in four or five individual corky diaspores per carpel. It is proposed that the corky layer has been selected for as a protection to the embryo in conjunction with the shift to salt water dispersal (cf. Stebbins, 1971).

Those species that lack appendages on the corolla lobes have mericarps that are terete and covered by an indument. The paired mericarps of *C. pubiflorum* may have as many as 16 segments each, and have a short, tomentose indumentum (Fig. 9C). The mericarps of *C. amazonicum* are single-seeded, fusiform, tapering to filiform extensions at both ends, and are covered by velutinous, ferruginous-brown hairs (Fig. 2G). An exception is *C. myrtifolium.* In this species the corolla lobes lack appendages, but the fruit is glabrous and flattened, and degeneration during development results in a one-carpellate, single-seeded fruit at maturity (Fig. 2H).

The seeds are fusiform, longitudinally folded and measure from 8.0 to 10.0 mm in length. The

testa is verrucose (Fig. 2I, J). The embryo is straight; the cotyledons are narrowly elliptic and constitute slightly more than half of the entire length of the embryo.

Pollen

Condylocarpon is one of the eight genera of Apocynaceae that are known to have pollen in tetrads (Erdtman, 1952). The tetrads are surrounded by a substance that stains deep blue in safranin and astra blue.

Infrageneric Relationships

The species of *Condylocarpon* can be separated into two basic groups. The first group is characterized by having the left margin of the corolla lobe elaborated into a lorate appendage with reddish brown markings on its abaxial surface. All of the species in this group have a simple orbicular style-head and glabrous, distinctly flattened or angled, articulated fruits. This is the larger group and includes *C. glabrum, C. guyanense, C. intermedium,* and *C. isthmicum.*

The second group is comprised of the two Amazonian endemics, *C. amazonicum* and *C. pubiflorum.* In this group the corolla lobes are auriculate or oblique and lack lorate appendages, and the style-head is turbinate. The fruits are covered by an indumentum and the segments are terete. It may seem that the single-seeded mericarps of *C. amazonicum* show little resemblance to the many-seeded mericarps of *C. pubiflorum,* but the similarity of their floral structure indicates a very close relationship between these two species, and at the same time distinguishes them from all other species in the genus.

Condylocarpon myrtifolium shows characteristics of both groups. The corolla lobes lack lorate appendages; they are auriculate and most closely resemble those of *C. amazonicum.* Although the style is relatively long, the style-head is simple and orbicular. One mericarp aborts during development, so that the fruit is a single, one-seeded mericarp composed of one glabrous, flattened segment.

Methods

Morphological studies were done with the aid of a Wild stereoscope and a Wild microscope, both with drawing-mirror attachments for illustrations.

Only dried herbarium specimens were available for study. Material to be studied in serial sections was first boiled for 3–4 minutes, to restore pliability and form, and then put into a dilute KOH solution and kept at 62°C for 1 hour. To remove the KOH the material was then placed in water and kept at 62°C at least 4 hours; this step was repeated. Specimens were then dehydrated in an alcohol-xylol series, embedded in paraplast, cut with a rotatory microtome at 10 micrometers, and stained with safranin and astra blue.

Specimens for study were provided on loan by the following herbaria: A, BM, BR, CAY, F, FI, G, GH, GOET, K, M, MO, NY, P, RB, S, U, UC, US, W, and Z. Unless otherwise stated, all type specimens were seen.

Taxonomic Treatment

Condylocarpon Desf. Mém. Mus. Hist. Nat. 8: 119. 1822. TYPE: *C. guyanense* Desf.

Maycockia A. DC., Prod. 8: 380. 1844. TYPE: *M. rauwolfiae* A. DC. ≡ *Condylocarpon rauwolfiae* (A. DC.) Muell.-Arg. ≡ *Echites isthmica* Vell. ≡ *Condylocarpon isthmicum* (Vell.) A. DC.
Hortsmania Miq., Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2, 7: 167. TYPE: *H. myrtifolia* Miq. ≡ *Condylocarpon myrtifolium* (Miq.) Muell.-Arg.
Rhipidia Mgf., Notizbl. Bot. Gart. Dahlem 10: 1033. TYPE: *Anechites* (?) *amazonica* Mgf. ≡ *Condylocarpon amazonicum* (Mgf.) Ducke.

Woody *lianas* with slender, lenticellate twigs with copious, milky latex. *Leaves* entire, membranous to subcoriaceous, decussate or verticillate, glabrous to subglabrous on the upper surface, glabrous to tomentose on the lower surface; petioles glabrous or with an indumentum. *Inflorescence* a many-flowered thyrse, becoming congested in the terminal branchlets; bracteoles small, ovate to triangular, glabrous to tomentose, usually ciliate. *Flowers* 2.5–5.0 mm long; calyx 5-lobed, the lobes obtuse to triangular, ciliate, often hyaline, inner surface without glands; corolla white, yellow or orange, funnelform or salverform, often globose in bud, aestivation sinistrorse, lobes oblique or with red-brown streaked, lorate appendages on the left margin; stamens 5, lanceolate to ovate, without sterile basal appendages and not adherent to the style-head, inserted near mid-tube or above, filaments short; ovary apocarpous, bicarpellate; style short; style-head orbicular, or turbinate, shortly bilobed at the apex. *Fruit* bifid, glabrous or with an indumentum, articulated into several one-seeded, indehiscent segments (in *C. myrtifolium,* reduced by degeneration during development to a soli-

tary, one-seeded segment), or filiform and not conspicuously articulated, and with only a single seed developing per carpel; seed 8.0–10.0 mm long, fusiform, longitudinally folded, testa verrucose; embryo straight, cotyledons narrowly elliptic. *Pollen* in tetrads.

Distribution: *Condylocarpon* comprises 7 species that occur principally in Brazil and the Guianas, with one species reaching Central America.

KEY TO THE SPECIES OF *CONDYLOCARPON*

1a. Corolla lobes with red-brown markings and lorate appendages; fruiting carpels distinctly articulated, flattened or angled in transverse section, glabrous; leaves opposite or verticillate.
  2a. Leaves 3 (occasionally 4) per node.
    3a. Markings not on petal appendages, but pale markings on petals; leaves glabrous on both surfaces; secondary veins 9–11 pairs ...... 3. *C. guyanense*
    3b. Markings mostly restricted to petal appendages; lower surface of leaves with patches of pubescence in axils of secondary veins, or tomentose; secondary veins 6–9 pairs ...... 5. *C. isthmicum*
  2b. Leaves opposite.
    4a. Corolla tube darker from base to level of stamen insertion; lower surface of leaves sparsely pilose along the midvein; secondary veins often difficult to distinguish from inter-secondary veins ...... 4. *C. intermedium*
    4b. Corolla tube not darker at the base; leaves glabrous on both surfaces, without inter-secondary veins ...... 2. *C. glabrum*
1b. Corolla lobes with neither red-brown markings nor lorate appendages; fruiting carpels terete and with an indumentum or, if glabrous, then fruit consisting of a single one-seeded mericarp; leaves opposite.
  5a. Fruit comprised of two carpels, with an indumentum; leaves sparsely to densely tomentose beneath; branches with a slight to dense golden-brown indumentum.
    6a. Petioles 2.0–6.0 mm long; flowers 4.0–5.0 mm long, corolla lobes 2.0–5.0 mm long, ovules arranged in four or five rows; fruit articulated into several one-seeded, indehiscent, pubescent segments ...... 7. *C. pubiflorum*
    6b. Petioles 0.5–1.0 mm long; flowers 3.5–4.0 mm long, corolla lobes 1.0–1.8 mm long, ovules arranged biserially; fruit with only one seed developing per carpel, covered by long, spreading ferruginous-brown hairs ...... 1. *C. amazonicum*
  5b. Fruit consisting of one flattened, one-seeded, glabrous carpel; leaves entirely glabrous; branches glabrous or puberulous in younger parts ...... 6. *C. myrtifolium*

1. Condylocarpon amazonicum (Mgf.) Ducke, Trop. Woods 76: 28. 1943. *Anechites* (?) *amazonica* Mgf., Notizbl. Bot. Gart. Dahlem 9: 960. 1926. *Rhipidia amazonica* (Mgf.) Mgf., Notizbl. Bot. Gart. Dahlem 10: 1033. 1930. TYPE: Brazil, Pará, Villa Braza, Tapajoz, *Ducke RB 17480* (fruiting) (RB, lectotype; MO, isolectotype). The holotype was destroyed at Berlin in 1943; the isotype is here designated as the lectotype.—Fig. 4A–E.

Condylocarpon reticulatum Ducke, Trop. Woods 76: 28. 1943. TYPE: Brazil, Amazonas, Esperança, mouth of Río Javari, Igarapé, *Ducke 1172* (flowering) (MG, holotype; MO, NY, isotypes).
Condylocarpon occidentale Mgf., Bradea 3: 80. 1980. TYPE: Brazil, Amazonas, Porto Velho-Guijará mirim, frontier Brazil-Bolivia, *Cordeiro 828* (flowering) (Z, holotype; INPA, isotype, not seen).

High climbing, woody *lianas*; branches terete, reddish brown infused with black, glistening, golden verrucose or lenticellate, subglabrous to golden-brown tomentose. *Leaves* opposite, elliptic to broadly lanceolate, subcoriaceous, 7.0–12.0 cm long, 2.5–5.0 cm broad, acute to shortly acuminate at the apex, obtuse to truncate at the base, the upper surface glabrous to subglabrous, the lower surface subglabrous to densely tomentose; secondary veins 12–15 pairs, prominent on the lower surface; midvein plane to shallowly canaliculate above, prominent below; petioles 0.5–1.0 cm long, shallowly canaliculate, often blackened and glistening, glabrous or with an indumentum. *Inflorescence* terminal and axillary thyrses, puberulous to densely reddish brown tomentose or velutinous; bracteoles lanceolate, acute, puberulous to tomentose. *Flowers* 3.5–4.0 mm long, 2.5–3.0 mm broad; pedicels slender, 0.5–2.0 mm long, subglabrous; calyx subglabrous to tomentose, lobes ovate to triangular, ciliate; corolla greenish white to creamy yellow, salverform, tube 2.0 mm long, 0.5–1.0 mm broad, constricted at the base, with an annular constriction at the throat, lobes 1.0–1.8 mm long, 0.7 mm broad, ascending to spreading, oblique, with neither lorate appendages nor red-brown markings; stamens ovate, inserted above mid-tube; ovary conical, ca. 0.6 mm long; style-head subsessile, turbinate; ovules four per carpel, biserially arranged. *Fruit* bifid, woody, densely velu-

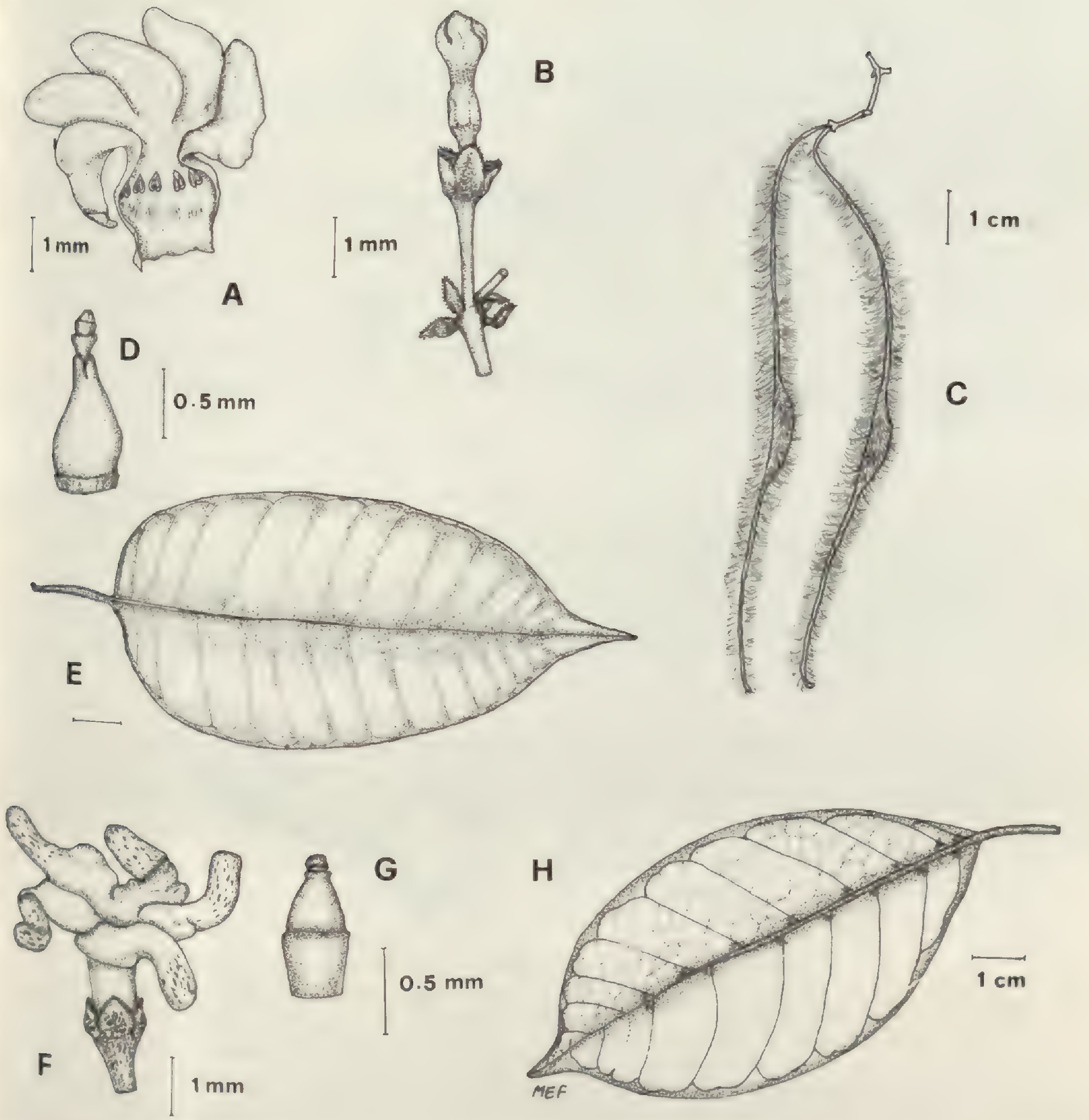

FIGURE 4. A–E, *Condylocarpon amazonicum*: A, corolla; B, flower in bud; C, fruit; D, gynoecium; E, leaf, upper surface. F–H, *Condylocarpon glabrum*: F, flower; G, gynoecium; H, leaf, lower surface.

tinous with spreading ferruginous-brown hairs 3.0–5.0 mm long, each carpel 10.5–15.0 cm long, filiform, terete, with only one seed developing per carpel, seed region enlarged, ca. 1.5 cm long, 3.0 mm broad.

Distribution: Secondary and riverine non-inundated forest in central and western Amazonian Brazil and adjacent regions in Venezuela, Suriname, and Bolivia (Fig. 5).

Specimens examined. VENEZUELA. AMAZONAS: *Breteler 4753* (F, M, MO, Z). SURINAME: *Heyde & Lindeman 65* (U); *190* (U); *Irwin et al. 55022* (K, NY, U). BRAZIL. AMAZONAS: *Chagas 416* (MO); *Cid et al. 825* (WAG); *925* (WAG); *Ducke 353* (A, F, K, MO, NY, US); *699* (F, MO, NY, US); *974* (K, MO, NY, UC, US); *2344* (NY, Z); *RB 21697* (K, P, RB, S, U, US; F, photo of sheet at P); *RB 23876* (K, U, US); *Krukoff 8007* (A, BR, F, K, MO, NY, U, US); *Prance et al. 14230* (F, K, M, NY, S, U, US); *14708* (F, GH, K, U, NY, S, US); *Rodrigues & Coelho INPA 7632* (F, MO). ACRE: *Forero 6317* (NY, Z). PARÁ: *Fróes 30423* (MO, US); *Oliveira 3610* (NY); *Silva 936* (F, NY, Z); *1419* (WAG). RONDÔNIA: *Cordeiro 136* (MO); *594* (Z); *828* (Z); *Prance et al. 5627* (F, K, NY, U, US, Z). BOLIVIA. PANDO: *Rusby 2599* (NY, US).

This species is distinct from all other species

FIGURE 5. Geographical distribution of *Condylocarpon*. Square = *C. amazonicum*; star = *C. glabrum*; triangle = *C. myrtifolium*; circle = *C. isthmicum*.

of *Condylocarpon* by the fruit, which is bicarpellate, but with only one seed developing per carpel, and by the filiform carpels, which are covered with long, stiff, ferruginous-brown hairs.

2. **Condylocarpon glabrum** Muell.-Arg. in Martius, Fl. Bras. 6(1): 66. 1860. TYPE: Brazil, Rio de Janeiro/Espírito Santo, between Campos and Vitória, *Sellow 304* (flowering) (K, lectotype; F, photo of isotype at B that was destroyed in 1943). A lectotype is chosen here because Muell.-Arg. did not choose a holotype.—Fig. 4F–H.

Woody *lianas* (?); the young branches puberulous, deep reddish brown infused with black, glistening, striate, lenticellate, becoming glabrous, densely lenticellate and streaked with golden-brown. *Leaves* opposite, becoming crowded at branch apex, elliptic to oblong-elliptic, membranous, 9.0–11.0 cm long, 3.0–5.0 cm broad, apex abruptly acuminate with acumen 5.0 mm long, acute to obtuse at base, glabrous on both surfaces, opaque on the upper surface, slightly paler on the lower surface, margins revolute; secondary veins 9 or 10 pairs, without inter-secondary veins, impressed and distinct adaxially, arching and becoming less distinct at the margin, prominent abaxially; midvein impressed on the upper surface, prominent on the lower surface; tertiary venation indistinct on the upper surface, reticulate and polygonally areolate on the lower surface; petioles 1.0–1.7 cm long, canaliculate, blackened, glabrous. *Inflorescence* a terminal thyrse, primary branches lax, 3.0–4.0 cm long, deep reddish brown, lenticellate, minutely puberulous, terminal branchlets congested; bracteoles subglabrous, ovate, acute, densely ciliate, 1.0–1.5 mm long. *Flowers* densely aggregated at the ends of the terminal branchlets, 2.5 mm long, globose in bud, subsessile or with pedicels up to 1.5 mm long; calyx glabrous, tube densely mottled with red-brown markings, lobes pallid, hyaline, broadly orbicular, margins ciliate; corolla pale, glabrous, funnelform, tube ca. 1.5 mm long, 1.0 mm broad, lobes with spreading, lorate petal appendages, ca. 1.0 mm long, 0.6 mm broad, that are densely speckled with deep red-violet to red-brown markings on the abaxial surface; stamens lanceolate, deep red-brown, inserted at mid-tube; ovary conical, bicarpellate, 0.3 mm long; style-head subsessile, round; ovules four per carpel, biserially arranged. *Fruit* unknown.

Distribution: Known only from the type, collected from the Atlantic coastal forest of Brazil, between Campos and Vitória (Fig. 5).

Condylocarpon glabrum shows affinities to *C. intermedium,* but differs by the pallid, broadly orbicular calyx lobes, in not having the lower portion of the corolla tube darkened, and with leaves which lack inter-secondary veins.

3. **Condylocarpon guyanense** Desf., Mém. Mus. Hist. Nat. 8: 119. 1822. TYPE: French Guiana, Cayenne, *Martin s.n.* (fruiting) (FI, holotype; P, isotype; F, NY, photo of isotype at B (destroyed in 1943), P, photo of holotype).—Fig. 6A–D.

Climbing, woody *lianas*; branches terete, reddish brown, lenticellate, at least the younger portions puberulous. *Leaves* three per node, elliptic to oblong-elliptic, membranous to subcoriaceous, 9.0–13.0 cm long, 3.0–4.5 cm broad, subcaudate to narrowly acuminate at apex, with acumen 1.0 cm long, 1.5–2.5 mm broad, acute at the base, glabrous on both surfaces; secondary veins 9–11 pairs, impressed on the upper surface, plane on the lower surface; midvein canaliculate on the upper surface, prominent on the lower surface, often with inter-secondary veins that diverge from the midvein but anastomose with tertiary venation; lower surface conspicuously reticulate with well developed, polygonal areoles with branched veinlets; petioles 1.2–1.8 cm long, canaliculate, puberulous. *Inflorescence* lax terminal and axillary thyrses, with primary branchlets 4.0–9.0 cm long, spreading, puberulous to pubescent; bracteoles ca. 1.0 mm long, acute, puberulous, ciliate. *Flowers* ca. 3.0 mm long, subsessile or with a slender pedicel up to 3.0 mm long; calyx pubescent, lobes ovate, densely ciliate; corolla creamy yellow to orange, salverform, glabrous, tube 1.5 mm long, 0.6–0.8 mm broad, lobes ca. 1.0 mm long, 0.5 mm broad, with lorate appendages, brown markings restricted to bases of lobes; stamens lanceolate, inserted at mid-tube; ovary conical, bicarpellate, 0.5 mm high; style-head orbicular, subsessile, ovules four or five per carpel, biserially arranged. *Fruit* apocarpous, reddish brown, glabrous, composed of two woody carpels, each articulated into as many as five one-seeded, indehiscent segments, each segment 1.5–2.5 cm long, 7.0 mm broad, somewhat flattened, striate, with a longitudinal streak over the seed area.

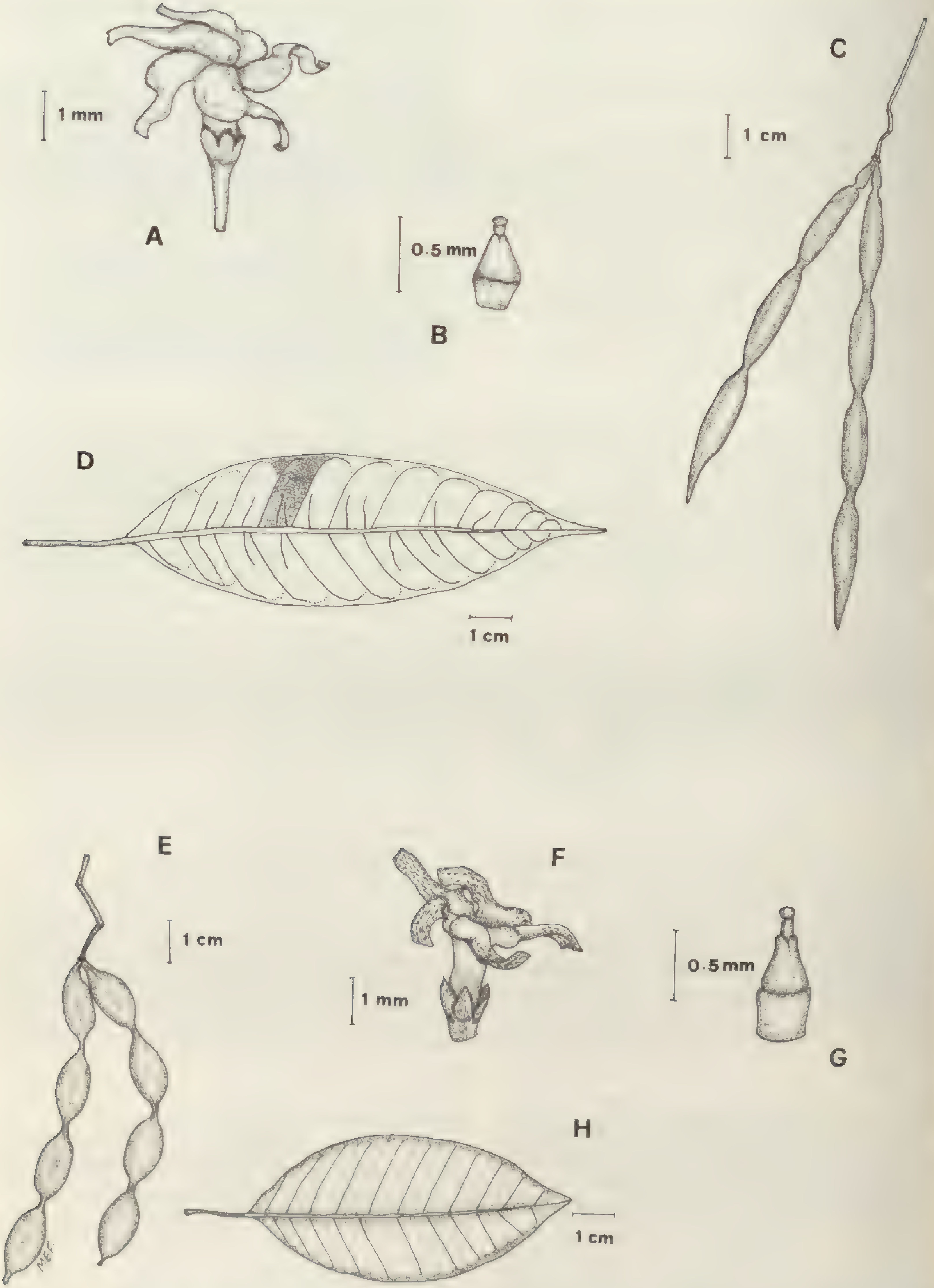

FIGURE 6. A–D, *Condylocarpon guyanense*: A, flower; B, gynoecium; C, fruit; D, leaf, lower surface. E–H, *Condylocarpon intermedium* subsp. *intermedium*: E, fruit; F, flower; G, gynoecium; H, leaf, upper surface.

FIGURE 7. Geographical distribution of *Condylocarpon*. Star = *C. guyanense*; black square = *C. intermedium* subsp. *intermedium*; white square = *C. intermedium* subsp. *laxum*; triangle = *C. pubiflorum*.

Distribution: Lowland forest in the Guianas to Terr. Amapá in Brazil (Fig. 7).

Specimens seen. GUYANA. *Forest Dept. Br. Gui. 83* (K); *Maguire 22890* (MO, NY). FRENCH GUIANA. *Lescure 531* (CAY, P); *Oldeman 1125* (CAY); *Prevost 514* (CAY); *Sastre 4701* (MO); *Sastre 5470* (CAY); *Sastre 5906* (CAY). BRAZIL. TERR. AMAPÁ: *Irwin 48275* (F, NY, U, Z); *Pires 50683* (NY).

4. **Condylocarpon intermedium** Muell.-Arg. in Martius Fl. Bras. 6(1): 65. 1860. TYPE: Guyana, banks of Pomaroon River, *Schomburgk 785* (flowering) (BM, lectotype; G, K, isolectotypes, here designated); *Schomburgk 1426* (flowering) (F, NY, photo of syntype at B that was destroyed in 1943).—Fig. 6E–H.

Condylocarpon intermedium var. *brevifolia* Muell.-Arg. in Martius Fl. Bras. 6(1): 65. 1860. TYPE: Brazil, Minas Gerais ?, *St. Hilaire s.n.* (flowering) (P, lectotype; F, isolectotype). A lectotype is chosen here, because Muell.-Arg. did not designate a holotype.

Condylocarpon obtusiusculum Muell.-Arg. in Martius Fl. Bras. 6(1): 65. 1860. TYPE: Brazil, Bahia, *Blanchet 1576* (flowering) (G, lectotype here designated). Brazil, without locality, *Sellow s.n.* (fruiting) (BM, paralectotype). Pro parte quoad plantam syntypicam, non *Silva da Manso s.n.*

Condylocarpon breviarticulatum Muell.-Arg. in Martius Fl. Bras. 6(1): 65. 1860. TYPE: Brazil, between Bahia and Vittoria, *Sellow 571* (fruiting) (K, lectotype; BM, F, isolectotypes, here designated).

Condylocarpon longii Standl. & Wms., Ceiba 3: 34. 1952. TYPE: Nicaragua, Dept. Zelaya, Bluefields, *Long 132* (flowering) (ENAG, holotype not seen; F, NY, US, isotypes; F, NY, photo of isotype at US). Nicaragua, Dept. Zelaya, Bluefields, Río Escondido, *Molina 1806, 1814* (ENAG paratypes not seen); Nicaragua, along Río Tanten, *Molina 2081* (flowering & fruiting) (BM, ENAG not seen, F, paratypes).

Slender, woody *lianas*; branches subverrucose or lenticellate, greyish, glabrous or puberulent in younger portions. *Leaves* opposite, ovate-elliptic to oblong-elliptic, membranous to subcoriaceous, 6.5–10.0 cm long, 2.8–4.5 cm broad, acute to obtuse at apex, obtuse to rounded at base, glabrous on the upper surface, glabrous on the lower surface except along the midvein, which is sparsely pilose; midvein impressed to subcanaliculate on upper surface, prominent on lower surface; secondary veins 9–13 pairs, plane and somewhat indistinct on upper surface, prominent on lower surface, often difficult to distinguish from inter-secondary veins; petioles 0.5–1.5 cm long, puberulous to glabrous, shallowly canaliculate to terete. *Inflorescence* rather lax terminal and axillary thyrses, branchlets puberulous to glabrous; bracteoles ovate to acute, hyaline, ciliate. *Flowers* 2.5–3.0 mm long, 3.5–4.0 mm broad, globose in bud, subsessile or with slender pedicels up to 2.0 mm long; calyx puberulous to glabrous, brown-speckled, lobes ovate to acute, hyaline, ciliate; corolla white, yellow or orange, with a darker region from the base extending to ca. the level of stamen attachment; tube 1.0–1.5 mm long, funnelform, base constricted, throat 1.5 mm broad; lobes 1.0–1.5 mm long, 0.6–0.8 mm broad, with spreading lorate appendages with reddish brown markings on their abaxial surface; stamens lanceolate, inserted at mid-tube; ovary apocarpous, conical; style-head orbicular, subsessile, or with a very short style, ovules five or six per carpel, biserially arranged. *Fruit* glabrous, composed of two woody carpels, each articulated into up to five one-seeded, indehiscent segments, each segment ovoid, 1.0 cm long, 0.7 cm broad, with a corky inner layer ca. 3–4 mm thick.

Key to the Subspecies

1a. Inflorescence about the same length as the leaves .... a. subsp. *intermedium*
1b. Inflorescence 2–3 times longer than the leaves .... b. subsp. *laxum*

a. Condylocarpon intermedium subsp. **intermedium.**

Inflorescence about the same length as the leaves; branchlets brownish grey.

Distribution: Coastal forests in Nicaragua, Trinidad, Venezuela, Guyana, and in Brazil, from Bahia to Rio de Janeiro (Fig. 7).

Specimens seen. VENEZUELA. DELTA AMACURO: *Steyermark et al. 114448* (MO, Z). TRINIDAD. *Baker TRIN 14568* (K); *Crueger s.n.* (K); *Finlay 2767* (NY). GUYANA. *Beckett s.n.* (K); *De La Cruz 4117* (F, MO, NY); *For. Dept. Br. Gui. 315* (K); *5066* (K, MO, NY, U); *5193* (F, K, MO, NY, U); *Hitchcock 17519* (NY); *Jenman 6173* (K, NY); *Ward & Kortright 8729* (K). BRAZIL. BAHIA: *Pinheiro 2147* (P, Z). ESPÍRITO SANTO: *Kuhlmann 6411* (Z). RIO DE JANEIRO: *Brade 11055* (RB); *Martinelli 4184* (Z); *Mello RB 49349* (MO, Z); *Schwache 3100* (GOET).

b. Condylocarpon intermedium subsp. **laxum** (Muell.-Arg.) Fallen, stat. nov.—*Condylocarpon laxum* Muell.-Arg. in Martius, Fl. Bras. 6(1): 66. 1860. TYPE: Brazil, Rio de Janeiro, Serra Tingua, *Schott 5478* (flowering) (W, lectotype; F fragment, M, NY, isolectotypes). Brazil, Porto da Estrella, *Riedel s.n.* (flowering) (G, P, paralectotypes; F, NY, photo of syntype at B, which was destroyed in 1943). A lectotype is chosen here from among the syntypes, since Muell.-Arg. did not designate a holotype.

Condylocarpon gracile Miers, Apocyn. S. Amer. 28. 1878. TYPE: Brazil, Rio de Janeiro, *Miers 4019 8086* (flowering, fruiting) (BM, holotype; NY, photo of isotype at B that was destroyed in 1943).

Inflorescence two to three times as long as the leaves, lax and spreading; branchlets glossy black.

Distribution: known only from Rio de Janeiro (Fig. 7).

Specimens seen. BRAZIL. RIO DE JANEIRO: *Gaudichaud s.n.* (F, NY, photo of specimen at B, since destroyed); *Kuhlmann 3788* (RB); *RB 39290* (Z). Without exact locality: *Raddi s.n.* (G).

5. Condylocarpon isthmicum (Vell.) A. DC., Prod. 8: 381. 1844.—*Echites isthmica* Vell., Fl. Flum. 3: 112. 1829 (1825), Icones 3: t. 39. 1831 (1827); reprinted in Arq. Mus. Nac. Rio de Janeiro 5: 106. 1881. TYPE: Brazil, Santa Crucis and Pharmacopolitanis, illustration in Fl. Flum. Icon. 3: t. 39.—Fig. 8A–D.

Condylocarpon rauwolfiae (A. DC.) Muell.-Arg. in Martius Fl. Bras. 6(1): 64. 1860.—*Maycockia rauwolfiae* A. DC., Prod. 8: 324. TYPE: Brazil, near Rio de Janeiro ?, *Lhotsky s.n.* (flowering) (G-DC, holotype; P, isotype; F, NY, photo of holotype).
Condylocarpon rauwolfiae var. *acuminata* Muell.-Arg. in Martius Fl. Bras. 6(1): 64. 1860. TYPE: Brazil, Prov. Minas Gerais, *Widgren 64* (fruiting) (BR, lectotype; M, P, S, U, isolectotypes). *192* (flowering) (GOET, P, S, paralectotypes). *1236* (flowering) (BR, paralectotype); *Riedel 85* (G, M, P, U, paralectotypes); *Langsdorff s.n.* (B, paralectotype, destroyed in 1943). Brazil, Prov. São Paulo, *St. Hilaire 1227* (flowering) (P, paralectotype);

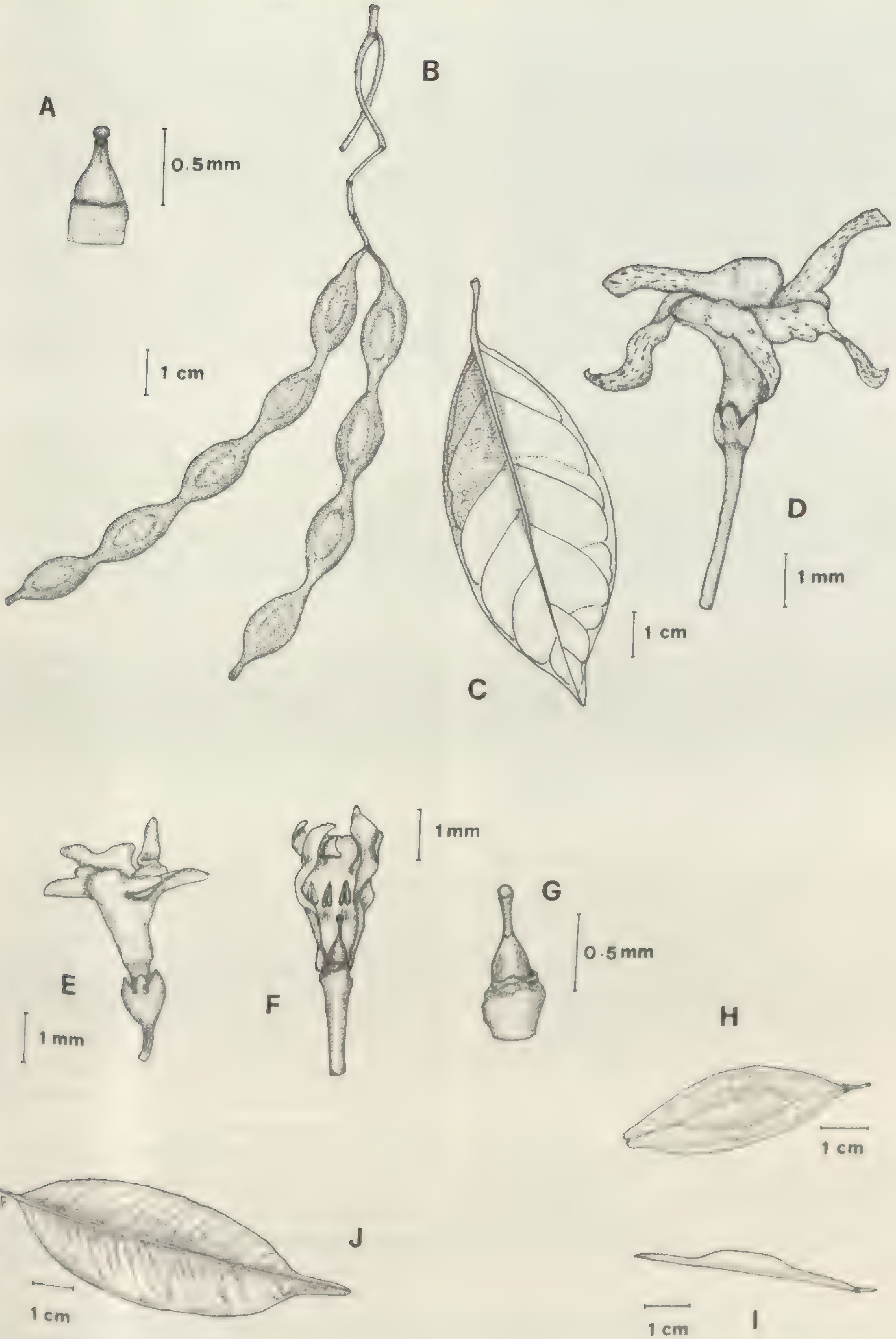

FIGURE 8. A–D. *Condylocarpon isthmicum*: A, gynoecium; B, fruit; C, leaf, lower surface; D, flower. E–I, *Condylocarpon myrtifolium*: E, flower, opened; G, gynoecium; H, fruit, top view; I, fruit, side view.

low s.n. (flowering) (BR, K, paralectotypes); *Gaudichaud 366* (flowering) (P, paralectotype), all here designated.

Condylocarpon rauwolfiae var. *tomentosa* Muell.-Arg. in Martius Fl. Bras. 6(1): 64. 1860. TYPE: Brazil, São Paulo, São Carlos, *Manso da Silva 335* (fruiting) (BR, lectotype); Brazil, Mato Grosso, *Martius s.n.* (fruiting) (M, paralectotype). One of the two syntypes is here chosen as a lectotype, because a holotype was not designated by Muell.-Arg.

Condylocarpon obtusiusculum Muell.-Arg. in Martius Fl. Bras. 6(1): 65. 1860. Pro parte quoad plantam syntypicam tantum Brazil, Mato Grosso, Cuiaba, *Manso da Silva s.n.* (flowering) (BR, lectotype, here designated).

Large, woody *lianas*; branches terete, lenticellate, glabrous or pubescent in younger portions. *Leaves* verticillate (mostly three per node), elliptic to ovate-elliptic, membranous to subcoriaceous, 7.0–11.5 cm long, 2.5–4.0 cm broad, acute to acuminate at apex, acute to obtuse at base, upper surface glabrous to subglabrous, lower surface glabrous with patches of pubescence in the axils of the secondary veins or tomentose; secondary veins 6–9 pairs, impressed on the upper surface, prominent on the lower surface; midvein impressed or canaliculate on the upper surface, prominent on the lower surface; tertiary venation well developed on lower surface, reticulate, polygonally areolate with branched veinlets; petioles 0.9–1.5 cm long, glabrous to tomentose. *Inflorescence* a terminal thyrse, branches puberulous to tomentose; bracteoles ovate to triangular, hyaline, ciliate. *Flowers* 3.5 mm long, 6.0–7.0 mm broad, pedicels 1.0–4.0 mm long, glabrous to tomentose; flower buds globose; calyx glabrous to tomentose, tube with red-brown markings, lobes ovate, hyaline, ciliate; corolla cream, yellow, or pale orange, funnelform, tube 1.5–1.8 mm long, throat 1.0–1.5 mm broad, lobes with spreading lorate appendages on the left margin; appendages 2.0–3.0 mm long, 0.5–0.8 mm broad, with reddish brown markings on the abaxial surface; stamens ovate to lanceolate, inserted at midtube; ovary apocarpous; style-head orbicular, subsessile; ovules five or six per carpel, biserially arranged. *Fruit* glabrous, pendent, composed of two woody carpels, each articulated into several (usually four or five) one-seeded, indehiscent segments, each segment ellipsoid, 1.5–2.5 cm long, 1.0–1.5 cm broad.

Distribution: Secondary, gallery, and periodically inundated forest and *campos* in the Brazilian Planalto and margins, from Ceará to Argentina (Fig. 5).

Representative collections. BRAZIL. CEARÁ: *Eugenio 980* (RB); *981* (RB). GOIÁS: *Anderson 7822* (NY, Z); *8265* (F, K, MO, NY, RB); *Glaziou 21730* (BR, G, K, P); *Heringer 9915* (Z); *Irwin et al. 18542* (F, NY, US); *31786* (F, NY, Z). DIST. FEDERÁL: *Belém & Mendes 24* (NY, U); *Duarte 10185* (Z); *Heringer 9189* (Z); *Irwin et al. 8339* (NY, P); *9539* (F, K, MO, NY, RB, Z); *11141* (F, NY, P); *11420* (F, K, MO, NY, RB); *15357* (F, MO, NY, P); *15657* (F, K, MO, NY, RB); *15913* (F, NY); *Pires 58060* (NY, Z). BAHIA: *Harley et al. 19907* (Z); *Mori et al. 12327* (Z). MINAS GERAIS: *Barreto 914* (F); *5177* (MO, RB); *Davidse & Ramamoorthy 10814* (MO); *Duarte 3538* (Z); *9900* (RB); *Gardner 5074* (K); *Irwin et al. 20764* (K, MO, RB); *27417* (F, NY); *Krieger et al. 10846* (RB); *11373* (RB); *Lindberg 192* (RB); *Magalhães 1226* (MO); *Mexia 4680* (F, G, K, MO, NY, U, Z); *Regnell II-136* (BR, F, GOET, M, NY, P, U, Z); *Roth 1736* (RB); *St. Hilaire 172* (P); *Teodoro 750* (RB); *Warming s.n.* (K, NY). ESPÍRITO SANTO: *Kuhlmann 460* (Z). RIO DE JANEIRO: *Capell RB 82113* (Z); *Cunningham s.n.* (K); *Duarte & Pereira 1749* (MO, Z); *Ginzberger 53* (F); *Glaziou 4081* (G, K, P); *7758* (G, K, P); *13470* (F, K, P); *15223* (BR, G, K, NY, P); *Goes 262* (RB); *Goes & Constantino 435* (BM, MO, RB); *541* (RB); *Goes & Dionisio 992* (RB); *1032* (Z); *Kuhlmann RB 19123* (G, K, P, RB, U); *Lima & Brade 13242* (RB); *Marquete et al. 123* (Z); *Markgraf 10050* (RB); *Martinelli 1327* (Z); *3006* (Z); *Tavares 111* (M); *Vitorio RB 39291* (MO, Z). SÃO PAULO: *Ball s.n.* (K); *Barreto 1727* (F, MO); *Burchell 4246* (BR, K, P); *Edwall RB 119753* (RB); *Frasão RB 86684* (RB); *Hoshimoto 52* (RB); *St. Hilaire 1404* (P); *Wachsmund s.n.* (Z); *Wacket s.n.* (Z). PARANÁ: *Dusen 3410* (NY); *7063* (F, G, MO, NY); *7798* (G, MO); *9094* (MO); *10701* (BR, K, P, Z); *14851* (MO); *14873* (BR, F, K); *15716* (BM, F, K, MO, P, Z); *15911* (NY); *16455* (MO); *Hatschbach 2842* (Z); *12138* (Z); *12473* (Z); *12543* (Z); *13155* (K, Z); *14181* (Z); *17604* (F, MO); *17869* (NY, P, Z); *24222* (NY, Z); *25308* (NY, RB, Z); *26460* (Z); *26591* (Z); *39849* (MO, NY); *41759* (Z); *Hoehne RB 23421* (RB); *Joensson 461a* (BM, G); *1168a* (G); *Kuniyoshi 4091* (Z); *Lindeman 3306* (K, NY, Z); *5288* (K, NY, U); *5350* (F, U); *Pedersen 10994* (MO, NY, Z); *Pereira 5385* (Z); *Reitz & Klein 17430* (NY, P); *Smith et al. 14514* (F). SANTA CATARINA: *Mueller 130* (K); *Smith & Klein 11685* (MO, NY, RB); *13126* (F, K, P, Z); *13162* (NY, P). RIO GRANDE DO SUL: *Rosengurtt et al. 9433* (K). PARAGUAY. *Fiebrig 5838* (G, K, P); *Hassler 10926* (G). ARGENTINA. MISIONES: *Ekman 1587* (NY); *Meyer 5573* (U); *Pedersen 11931* (U, Z); *Schwarz 4215* (MO). ENTRE RIOS: *Troncoso 1379* (F, MO).

The type specimen of *Echites isthmica*, which was published in Vellozo's *Flora Fluminensis* (1829) was lost. Therefore, the type of the species becomes the plate in the *Flora Fluminensis*. In the case of *Echites isthmica* the plate is, at best, inadequate, and it is not without some apprehension that I say that *Condylocarpon rauwolfiae* is conspecific with *C. isthmicum*. However, the plant depicted in plate 39 of the *Flora Fluminensis* (1831) clearly has three leaves per node.

This, together with the fact that the specimen was collected in Rio de Janeiro, near Santa Cruz, almost certainly make it the same species as the type specimen of *C. rauwolfiae.*

The two varieties of *C. rauwolfiae, acuminata* and *tomentosa,* are not recognized in *C. isthmicum.* These varieties were circumscribed by Mueller-Argoviensis (1860) by leaf shape and the indumentum of the lower leaf surface, both of which show considerable variability, not only among individuals, but also from the same individual. There may be a two- or three-fold difference in leaf size, depending upon which part of the liana was used for the specimen, as well as upon the maturity of the leaves. In addition, there is a negative correlation between leaf size and latitude, from Ceará at about 5°S, to Rio Grande do Sul at about 27°S.

Condylocarpon isthmicum is similar to *C. intermedium* and *C. glabrum* in having the lorate, red-brown streaked petal appendages and glabrous, articulated fruit.

6. **Condylocarpon myrtifolium** (Miq.) Muell.-Arg. in Martius Fl. Bras. 6(1): 65. 1860.—*Hortsmania myrtifolia* Miq., Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem. ser. 2, 7: 167. 1851. TYPE: Suriname, without exact locality, *Hostmann 1196* (flowering) (U, lectotype; F, G, GOET, K, MO, NY, P, isolectotypes; F, photos of isolectotypes at G and P, NY, photo of isolectotype at G); *462* (flowering) (P, U, paralectotypes). One of the syntypes is here designated as a lectotype, because a holotype was not designated by Miquel.—Fig. 8E–I.

Slender, woody *lianas*; branches reddish brown, densely lenticellate, puberulous to glabrous, becoming silvery grey and glabrous with age. *Leaves* opposite, oblong-elliptic, membranous, 6.0–10.0 cm long, 2.0–3.5 cm broad, shortly caudate at apex, acumen 1.0 cm long, obtuse to rounded at base, glossy, glabrous on the upper surface, paler, and glabrous on the lower surface, margins plane; secondary veins 11–13 pairs, prominent on the upper surface, with numerous equally prominent inter-secondary veins diverging from the midvein, curving and anastomosing with sub-prominent, oblique tertiary venation or occasionally connecting with marginal collective vein. Midvein canaliculate on the upper surface, canal puberulous to glabrous, prominent on the lower surface; petioles 2.0–4.0 mm long, glabrous, canaliculate for about half this length. *Inflorescence* a short, very congested thyrse, glabrous or puberulous in younger branches; bracteoles ovate-triangular, puberulous, golden-brown, ciliate. *Flowers* 3.0–3.5 mm long, subsessile or with pedicels ca. 1.0 mm long; calyx puberulous to pubescent, lower portion darkened by reddish brown markings, lobes pale gold, ovate, apex acute, ciliate; corolla salverform, greenish white to creamy yellow, darker near the base; tube 2.0 mm long, 6.0 mm broad, minutely puberulous, constricted at the base, ca. 1.5 mm broad at the throat; lobes 1.0 mm long, 0.6 mm broad, shortly auriculate, ascending and slightly spreading, without lorate appendages or red-brown markings; stamens lanceolate, inserted at mid-tube; ovary conical, 0.3 mm long, darker than style; style 0.3 mm long, topped by an orbicular style-head; ovules four or five per carpel, biserially arranged. *Fruit* consisting of only one carpel (the second degenerating during development), a pendulous one-seeded, flattened, ellipsoidal disc with an apical notch, 4.0–5.0 cm long, 1.5–2.0 cm broad, greenish brown, leathery, with lateral veins diverging from the canaliculate central suture; seed area longitudinally striate, raised on the abaxial surface.

Distribution: Non-inundated forest in Suriname, Venezuela, and Amazonia (Fig. 5).

Specimens examined. VENEZUELA. DELTA AMACURO: *Bond 218* (NY). GUYANA. *De La Cruz 2850* (NY); *For. Dept. Br. Gui. 4146* (K, NY, U); *im Thurn s.n.* (K, P); *Jenman 88* (P); *243* (NY, P); *Tutin 162* (BM, RB, U). SURINAME. *Focke 958* (U); *Gonggrijp 120* (U); *Kegel 1009* (GOET); *Stahel & Gonggrijp 3000* (U); *Went 551* (U); *Wullschlaegel 1654* (BR). BRAZIL. PARÁ: *Black 48-3006* (RB); *Ducke 7382* (RB, U); *RB 15816* (RB); *RB 21592* (RB); *RB 21618* (RB); *RB 21620* (RB). TERR. RONDÔNIA: *Kuhlmann RB 21866* (RB, U); *Maguire et al. 56763* (F, NY, Z). BOLIVIA. PANDO: *Prance et al. 8654* (F, NY, P, U, Z); *Rusby 2391* (F, G, K, NY).

This species is easily recognized by the oblong, caudate-tipped leaves with numerous inter-secondary veins, and glossy upper surface, and the one-carpellate, inarticulated fruit.

7. **Condylocarpon pubiflorum** Muell.-Arg. in Martius Fl. Bras. 6(1): 67. 1860. TYPE: Brazil, Amazonas, mouth of Río Negro, *Spruce 1564* (flowering) (BR, lectotype; F, G, GOET, K, M, NY, P, isolectotypes; F, NY, photo of isolectotype at B that was destroyed in 1943).—Fig. 9.

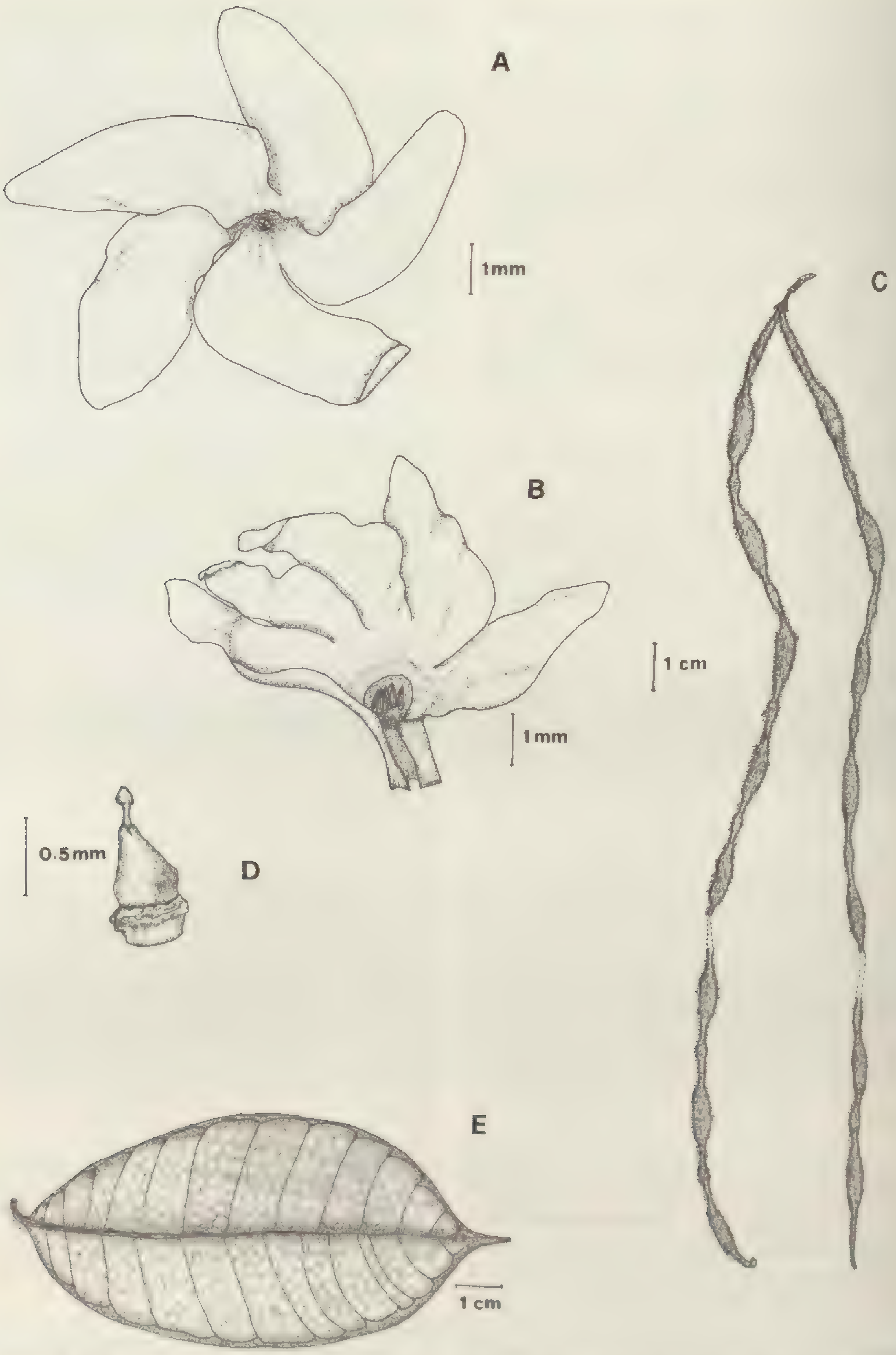

FIGURE 9. *Condylocarpon pubiflorum*: A, corolla, top view; B, opened corolla, side view; C, fruit; D, gynoecium; E, leaf, upper surface.

Condylocarpon ciliatum Muell.-Arg. in Martius Fl. Bras. 6(1): 66. 1860. TYPE: Amazonas, near Panuré [Ipanôre], Río Uaupés, *Spruce 2475* (flowering) (BR, lectotype; BM, G, K, NY, P, isolectotypes; F, photo of isolectotype at B that was destroyed in 1943).

Condylocarpon hirtellum Ducke, Trop. Woods 76: 28. 1943. TYPE: Brazil, Amazonas, Esperança, mouth of Río Javari, *Ducke 1171* (fruiting) (MG, holotype, not seen; NY, isotype).

Large, high-climbing, woody *lianas*; branches terete, reddish brown, somewhat blackened at nodes, golden verrucose or lenticellate, with a sparse indumentum of golden-brown hirsute hairs that is denser at the nodes. Leaves opposite, elliptic to oblong-elliptic, membranous, 6.5–15.0 cm long, 2.5–5.0 cm broad, narrowly acuminate to shortly caudate at apex, acumen 5.0–10.0 mm long, acute to rounded at the base, upper surface glossy, glabrous or with a very sparse scattering of golden-brown hirsute hairs, lower surface paler, glabrous or sparsely golden-brown tomentose, margins revolute; secondary veins 9–15 pairs, slightly impressed on upper surface, prominent and sparsely tomentose on the lower surface; midvein canaliculate on the upper surface, prominent on the lower surface, tomentose to velutinous on both surfaces; petioles 2.0–6.0 mm long, canaliculate, darkened, golden-brown tomentose to hirsute. *Inflorescence* a terminal thyrse, golden-brown puberulous to velutinous; bracteoles triangular, golden to ochre, puberulous to tomentose, persistent, congested and imbricate. *Flowers* 4.0–5.0 mm long, 6.0–9.0 mm broad, subsessile or with glabrous pedicels up to 2.0 mm long; calyx glabrous, lobes ovate, membranous, ciliate; corolla white to creamy yellow, salverform, tube 1.5–2.0 mm long, base constricted, throat ca. 1.0 mm broad, with an annular constriction, lobes spreading, 2.0–5.0 mm long, 1.0–2.0 mm broad, with neither lorate appendages nor red-brown markings. Stamens lanceolate, inserted near top of tube; ovary conical, ca. 0.8 mm long, style 0.3 mm long; style-head turbinate; ovules ca. 16 per carpel, arranged in four or five rows. *Fruit* apocarpous, densely golden tomentose, composed of two woody carpels, each indistinctly articulated into several (up to 16), one-seeded, indehiscent cylindrical segments, each segment 2.0–2.5 cm long, 2.0–3.5 mm broad.

Distribution: Non-inundated or periodically inundated forests in central and western Amazonia (Fig. 7).

Specimens seen. COLOMBIA. PUTUMAYO: *Cuatrecasas 10823* (F). AMAZONAS: *Schultes 6677* (US). VENEZUELA. AMAZONAS: *Liesner 3603* (MO); *Maguire et al. 36752* (F, MO, NY); *Morillo & Hasegawa 5165* (F). PERU. LORETO: *Gentry 21821* (F, MO, Z); *Revilla 321* (F, MO, Z); *1820* (MO); *Williams 2011* (F); *3770* (F). BRAZIL. AMAZONAS: *Ducke RB 22434* (G, P, RB, U); *RB 23938* (RB, U); *Fróes 21195* (NY); *Krukoff 6760* (NY); *8265* (NY); *Martius* (M); *Spruce 3417* (K).

The nearest relative of *C. pubiflorum* is *C. amazonicum*. The two species most closely resemble each other in the westernmost part of their ranges in Amazonian Peru, Colómbia, and Venezuela. Without mature flowers or fruit, specimens of these two species from this region can be very difficult to distinguish from each other.

Numerical List of Taxa

1. *Condylocarpon amazonicum* (Mgf.) Ducke
2. *Condylocarpon glabrum* Muell.-Arg.
3. *Condylocarpon guyanense* Desf.
4. *Condylocarpon intermedium* Muell.-Arg.
   a. subsp. *intermedium*
   b. subsp. *laxum* (Muell.-Arg.) Fallen
5. *Condylocarpon isthmicum* (Vell.) A. DC.
6. *Condylocarpon myrtifolium* (Miq.) Muell.-Arg.
7. *Condylocarpon pubiflorum* Muell.-Arg.

List of Exsiccatae

The figures in parentheses refer to the species number as given above in the numerical list of taxa. Collection year follows s.n., when available.

Anderson, W. R., 7822 (5); 8265 (5)
Baker, R. E. D., TRIN 14568 (**4a**)
Ball, J., s.n., 1882 (5)
Barreto, M., 914 (5); 1727 (5); 5177 (5)
Beckett, J. E., s.n., 1906 (**4a**)
Belém, R. P. et al., 24 (5)
Black, G. A., 48-3006 (6)
Blanchet, J. S., 1576 (**4a**)
Bond, F. E. et al., 218 (6)
Brade, A. C., 11055 (**4a**)
Breteler, F. J., 4753 (1)
Burchell, W. J., 3513 (5); 4246 (5); 5975 (5)
Capell, P., RB 82113 (5)
Chagas, J., 416 (1)
Chauso, S. et al., 78 (5)
Cid, C. et al., 825 (1); 925 (1)
Cordeiro, M. R. et al., 136 (1); 594 (1); 828 (1)
Crueger, H., s.n., 1860 (**4a**)
Cuatrecasas, J., 10823 (7)
Cunningham, A., s.n., 1867 (5)
De La Cruz, J. S., 2850 (6); 4117 (**4a**)
Duarte, A. P. et al., 1749 (5); 3538 (5); 9900 (5); 10185 (5)
Ducke, A., 353 (1); 699 (1); 974 (1); 1171 (7); 1172 (1); 2344 (1); 7382 (6); RB 15816 (6); RB 17480 (1); RB 21592 (6); RB 21618 (6); RB 21620 (6); RB 21697 (1); RB 22434 (7); RB 23876 (1); RB 23938 (7)

Dusen, P. K. H., 3410 (**5**); 7063 (**5**); 7798 (**5**); 9094 (**5**); 10701 (**5**); 14851 (**5**); 14873 (**5**); 15716 (**5**); 15911 (**5**); 16455 (**5**)
Edwall, G., RB 119753 (**5**)
Ekman, E. L., 1587 (**5**)
Engler, 65 (**5**); s.n., 1864 (**5**)
Eugenio, J., 980 (**5**); 981 (**5**)
Fiebrig, K., 5838 (**5**)
Finlay, Mrs. G. R., 2767 (**4a**)
Focke, H. C., 958 (**6**)
Fontella et al., 1118 (**5**)
Forero, E. et al., 6317 (**1**)
For. Dept. Br. Gui. (Guyana), 83 (**3**); 315 (**4a**); 4146 (**6**); 5066 (**4a**); 5193 (**4a**)
Frasão, A., RB 86684 (**5**)
Fróes, R. L., 21195 (**7**); 30423 (**1**)
Gardner, G., 5074 (**5**)
Gaudichaud, C., 366 (**5**); s.n. (**4b**)
Gentry, A. H. et al., 21821 (**7**)
Ginzberger, A. et al., 53 (**5**)
Glaziou, A. F. M., 4081 (**5**); 7758 (**5**); 7886 (**5**); 13470 (**5**); 15223 (**5**); 21730 (**5**)
Goés, O. C. et al., 262 (**5**); 435 (**5**); 541 (**5**); 992 (**5**); 1032 (**5**)
Gonggrijp, J. W., 120 (**6**)
Graham, Bro. Wm., s.n. (**5**)
Hanbury, G., 2 (**5**); 4 (**5**); s.n. (**5**); s.n., 1866 (**5**); s.n., 1868 (**5**)
Harley, R. M., 19907 (**5**)
Hassler, E., 10926 (**5**)
Hatschbach, G., 2842 (**5**); 12138 (**5**); 12473 (**5**); 12543 (**5**); 13155 (**5**); 14181 (**5**); 17604 (**5**); 17869 (**5**); 24222 (**5**); 25308 (**5**); 26460 (**5**); 26591 (**5**); 39849 (**5**); 41759 (**5**)
Heringer, E. P., 9189 (**5**); 9915 (**5**)
Heyde et al., 65 (**1**); 190 (**1**)
Hitchcock, A. S., 17519 (**4a**)
Hoehne, F. C., RB 23421 (**5**); RB 28439 (**5**)
Hoshimoto, A., 52 (**5**)
Hostmann, W. R. et al., 264 (**6**); 1196 (**6**)
Im Thurn, E., s.n., 1879 (**6**)
Irwin, H. S. et al., 8339 (**5**); 9539 (**5**); 11141 (**5**); 11420 (**5**); 15357 (**5**); 15657 (**5**); 15913 (**5**); 18542 (**5**); 20764 (**5**); 27417 (**5**); 31786 (**5**); 48275 (**3**); 66022 (**1**)
Jenman, G. S., 88 (**6**); 243 (**6**); 6173 (**4a**)
Joensson, G., 461a (**5**); 1168a (**5**)
Kegel, H., 1009 (**6**)
Krieger, P. L. et al., 10846 (**5**); 11373 (**5**)
Krukoff, B. A., 6760 (**7**); 8007 (**1**); 8265 (**7**)
Kuhlmann, J. G., 460 (**5**); RB 3788 (**4b**); 6411 (**4a**); RB 19123 (**5**); RB 21866 (**6**); RB 39290 (**4b**)
Kuniyoshi, Y. S., 4091 (**5**)
Lescure, 531 (**3**)
Lhotsky, J., s.n. (**5**)
Liesner, R., 3603 (**7**)
Lima, S. et al., 13242 (**5**)
Lindberg, G. A., 192 (**5**)
Lindeman, J. C., 3306 (**5**); 5288 (**5**); 5350 (**5**)
Long, L. E., 132 (**4a**)
Magalhães, M., 1226 (**5**)
Maguire, B. et al., 22890 (**3**); 36752 (**7**); 56763 (**6**)
Manso, A. L. P. da Silva, 335 (**5**); s.n., 1834 (**5**)
Markgraf, F., 10050 (**5**)
Marquete, N. et al., 123 (**5**)
Martin, J., s.n. (**3**)
Martinelli, G. et al., 1327 (**5**); 3006 (**5**); 4184 (**4a**); 8450 (**4a**)
Martius, K. F. P. von, s.n., 1819 (**5**); s.n. (**7**)
Mello, M., s.n. (**4a**)
Mexia, Y., 4680 (**5**)
Meyer, T., 5573 (**5**)
Miers, J., 4019 (**4b**); 8086 (**4b**)
Moliná, R. A., 2081 (**4a**)
Mori, S. et al., 12327 (**5**)
Morillo, G., 5165 (**7**)
Mosén, C. W. H., 621 (**5**); 3653 (**5**)
Mueller, F., 130 (**5**)
Oldeman, R. A. A., B1125 (**3**)
Oliveira, E., 3610 (**1**)
Pabst, G., 9065 (**5**)
Peckott, T., 350 (**5**)
Pedersen, T. M., 10994 (**5**); 11931 (**5**)
Pereira, E., 5385 (**5**)
Pinheiro, R. S., 2147 (**4a**)
Pires, J. M. et al., 50683 (**3**); 58060 (**5**)
Pohl, J. E., 651 (**5**)
Prance, G. T. et al., 5627 (**1**); 8654 (**6**); 14230 (**1**); 14708 (**1**)
Prévost, M. F., 514 (**3**)
Raddi, G., s.n. (**4b**)
Regnell, A. G., II-136 (**5**)
Reitz, P. R. et al., 17430 (**5**)
Revilla, J., 321 (**7**); 1280 (**7**); 1820 (**7**)
Riedel, L., 85 (**5**); s.n. (**4b**)
Rodrigues, W. A. et al., 1303 (**1**)
Rosengurtt et al., 9433 (**5**)
Roth, L., 1736 (**5**)
Rusby, H. H., 2391 (**6**); 2599 (**1**)
Saint Hilaire, A., 172 (**5**); 1227 (**5**); 1404 (**5**); s.n., 1816–1821 (**4a**)
Sastre, C., 4701 (**3**); 5470 (**3**); 5906 (**3**)
Schomburgk, R., 785 (**4a**); 1426 (**4a**)
Schott, H. W., 5478 (**4b**); 5479 (**5**)
Schwacke, C. A., 3100 (**4a**)
Schwarz, G. J., 4215 (**5**)
Sellow, F., 45 (**5**); 304 (**2**); 571 (**4a**); s.n., 1815–1817 (**4a**); s.n. (**5**)
Silva, N. T., 936 (**1**)
Smith, L. B. et al., 11685 (**5**); 13126 (**5**); 13162 (**5**); 14514 (**5**)
Spruce, R., 1564 (**7**); 2475 (**7**); 3417 (**7**)
Stahel, G. et al., 3000 (**6**)
Steyermark, J. et al., 114448 (**4a**)
Tavares, J., 111 (**5**)
Teodoro, T., 750 (**5**)
Troncoso, N. S., 1379 (**5**)
Tutin, T. G., 162 (**6**)
Tweedie, J., s.n. (**5**)
Vitório, RB 39291 (**5**)
Wachsmund, A., s.n., 1902 (**5**)
Wacket, M., s.n., 1902 (**5**)
Ward, R. et al., 8729 (**4a**)
Warming, J. E. B., s.n., 1864 (**5**)
Went, F. A. F. C., 551 (**6**)
Widgren, J. F., 64 (**5**); 192 (**5**); 1236 (**5**)
Williams, Ll., 2011 (**7**); 3770 (**7**)
Wullschlaegel, H. R., 1654 (**6**)

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SUPPLEMENT TO THE CONTRIBUTIONS TO THE SYNANTHROPIC (ADVENTIVE) FLORA OF THE RAILROADS IN ST. LOUIS, MISSOURI, U.S.A.[1]

VIKTOR MÜHLENBACH[2]

ABSTRACT

Based on 93 excursions from 1972–1980, 22 additional synanthropic species were discovered on the railroad network in St. Louis. Included were 13 new species and 3 new varieties for the flora of Missouri. In addition 37 taxa, native to Missouri but probably introduced into the St. Louis region, are discussed.

My summary paper on synanthropes of the railroads of St. Louis (Mühlenbach, 1979) was based only on fieldwork from 1954 through 1971. From 1972 through 1980 93 additional excursions were undertaken on the Missouri side of the Mississippi River. In addition, from 1978 through 1980 railroad premises and freight yards on the Illinois side of the Mississippi River were visited 38 times and the results were published by Shildneck, Jones, and Mühlenbach (1981). The synanthropic floras were very similar on both sides of the Mississippi River. Only three species were found in Illinois that were not encountered in St. Louis, *Draba verna* L., *Alliaria officinalis* Andrz., and *Geranium pusillum* Burm. f. A fourth species—*Mirabilis linearis* (Pursh) Heimerl, synanthropic in Illinois but native in Missouri—was found only in Illinois.

For this supplement only 22 new additional synanthropic species were discovered, compared to the 393 of the first report (Mühlenbach, 1979). Included among these new discoveries are plants collected during the earlier years but not fully identified until recently. Although the low percentage of new discoveries for the latter period can be expected after the initial 17 years of concentrated fieldwork, an additional factor also plays a part. This was the much greater use of herbicides. Traditionally many synanthropes have been discovered in the classification or switching tracks, areas where freight trains are rearranged for further movement. Most such areas are now devoid of vegetation throughout the year because of herbicide spraying. During the early years of my fieldwork the vegetation in the classification tracks was frequently not sprayed until the plants were knee-high. Then one would indeed find marvellous plants in abundance in those places. Such abundant plant growth is now seen only in exceptional cases. One case is reviewed later in detail.

RESULTS

Novelties for the state of Missouri are noted first. They include 13 species and 3 new varieties of known species. The names of the cited railroad companies are substituted by their official acronyms: BN (Burlington Northern); C&EI (Chicago & Eastern Illinois); MKT (Missouri-Kansas-Texas); MP (Missouri Pacific); MRS

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Finally, during this second period I enjoyed the company of many persons, mostly members of the Missouri Botanical Garden or students of Washington University, who brought me to the freight yards in their cars and also helped to collect. Important discoveries were also made by some of them. These persons are David Boufford, Jim Conrad, Rose Conrad, Dorothy England, Mary Fallen, Peter Hoch, Jack Humbles, Randy Hyman, Walter Lewis, Ilze Muehlenbachs, Karlis Muehlenbachs, Duncan Porter, Janice Saunders, Maburl Schober, Jim Solomon, Warren Wagner, Peter White, Emily Wood, and Vincent Zenger. Mr. A. P. Rennie and Mr. C. G. Pair of the Canadian National Railways helped with my work in Edmonton. I express my gratitude to all of them.

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(Manufacturers Railway); RI (Rock Island, now in the possession of St. Louis Southwestern Railway = Cotton Belt Route (SSW)); SL-SF (St. Louis & San Francisco Railway, now in the possession of BN); TRRA (Terminal Railroad Association of St. Louis).

Bromus japonicus Thunb. var. **grandis** Vel.
M 3830A, Carrie Ave. Fr. Yd. (RI), 28 June 1973, one specimen amidst a colony of the typical specimen of this species. Determined by H. Scholz. Bulgaria (Velenovský, 1898).

Bromus arvensis L.
M 4169, Carrie Ave. Fr. Yd. (RI), 4 July 1978, one colony. *M 4172*, Bulwer Yd. (TRRA), 4 July 1978, two specimens. Both collections determined by H. Scholz. Eurasia.

Echinochloa utilis Ohwi & Yabuno.
M 1577, Bremen Fr. Yd. (TRRA), 7 Sept. 1959, one specimen. *M 3349*, Lesperance St. Fr. Yd. (MP), 25 July 1970, one colony. Both collections were previously identified as *E. crusgalli* (L.) Beauv. The new identification follows the annotations of P. Michael (University of Sydney, N.S.W.). This species was first discovered in 1961 in Sakai, Province Izumi, Japan, and described as a new species by Ohwi and Yabuno in 1962 (Ohwi, 1962). A fuller morphological and geographical description is given by Yabuno (1966) and especially by Vickery (1975: 197), who noted that "prior to 1962 this species appears to have been widely confused with *E. frumentacea* of India . . . the two are totally distinct . . . . *E. utilis* doubtless originated in eastern Asia, including Japan, and is considered by Yabuno . . . and by Ohwi to have originated from *Echinochloa crusgalli* . . . . Cultivated for forage and grain and may be an occasional weed of cultivated areas . . . ."

Carex crawfordii Fern. (*C. scoparia* Schkuhr var. *minor* Boott).
M 3751, former Railway Exchange Agency (REA, 1730 Clark Ave.) leased from TRRA, 24 June 1972, one large, dense tuft. Determined by F. J. Hermann. It was most unusual and perplexing to find *C. crawfordii*. It is basically a northern species, frequent in Canada (Nfld.-B.C.) and in 10 of the 13 northern border states of the U.S.A. according to the literature and the herbarium material at MO. Only a few states are cited southwards. The nearest state to Missouri according to Fernald (1950) is Tennessee where it occurs in the high mountains. In the principal area of its distribution, Gleason (1968) characterizes the habitats as wet soil, meadows, swamps, and shores, places that very seldom produce synanthropes. Northern introductions are exceptional events, in Europe as well as in the U.S.A. The assumption that we are dealing with a native plant cannot be completely neglected, but the probability seems low. I (Mühlenbach, 1979) previously cited several synanthropes for which native status could not be completely ruled out. Nevertheless, I classified them as synanthropes because they grew in association with other rare synanthropes. I treat *C. crawfordii* likewise. It grew on the track along one of the loading platforms of the former REA, again in company of interesting and rare synanthropes. See Hermann (1970) for further details.

Salix alba L. × **S. fragilis** L. (*S.* × *rubens* Schrann).
M 2068 (flowers) and *M 2183* (leaves), from a unicate shrub, 7 April 1963 and 28 Aug. 1963, Harlem Fr. Yd. (TRRA). Determined by G. W. Argus. Eurasia.

Rumex cristatus DC. (*R. graecus* Boiss. & Heldr.).
M 725, SL-SF, west of Knox Ave., 14 Aug. 1955, one specimen. *M 3967*, SL-SF, west of Macklind Ave., near the Des Peres sewer, 5 July 1976, one specimen. *M 4028*, MP, at the branching of the siding from the trunk line to the RF Macaroni and Spaghetti Works, 30 May 1977, one small colony. *M 4060*, Lindenwood Fr. Yd. (SL-SF), 17 Sept. 1977, three small colonies. *M 4188*, Baden Fr. Yd. (MKT), 15 July 1978, one specimen. All collections determined by K. H. Rechinger. To the best of Rechinger's knowledge *R. cristatus* has not been found in the U.S.A. as an adventive plant. This species was treated by him in Hegi (1953) and in Jalas & Suominen (1979). Eastern Mediterranean. I succeeded also in discovering this plant in Illinois (*M 4224*, 4 Aug. 1978, along the Eastern Connection between the Madison Fr. Yd. of TRRA and that of the Chicago and North Western Railway of the same name). *Rumex orbiculatus* Gray, cited in Steyermark (1963: 580), turned out to be the first specimen of *R. cristatus* found in St. Louis (*M 725*).

Polygonum cuspidatum Sieb. & Zucc. var. **compactum** (Hook. f.) Bailey.
M 3356, MP, south of Zepp St., 30 July 1970, two specimens. *M 3476*, TRRA, west of Union

Blvd., 7 Nov. 1970, one colony. In both cases the plants were sterile. Determined by H. A. Wahl. Japan.

Brassica napus L. var. **napus** (*B. napus* L. var. *arvensis* (Lam.) Thellung).

M 100, between the right-of-ways of MP and SL-SF, west of the Kingshighway overpass, 29 May 1954, one specimen. Determined by H. Scholz. Known only as a cultigen (rape, an oil and forage plant).

Brassica oleracea L.

M 1565, North St. Louis Fr. Yd. (BN), 23 Aug. 1959, one specimen (B). *M 2088,* Carrie Ave. Fr. Yd. (RI) or Bulwer Yd. (TRRA), 30 May 1963, one or two? specimens. Both determined by H. Scholz. Widely cultivated vegetable, originating in the Mediterranean.

Reseda lutea L.

M 3931, Carrie Ave. Fr. Yd. (RI), 12 June 1976, one specimen. Determined by H. Scholz. Eurasia. This species is missing in Steyermark's *Flora of Missouri,* while Fernald (1950) cites Missouri among states in which *R. lutea* is introduced. As I stated earlier (Mühlenbach, 1979), Steyermark's (1963) *Flora of Missouri* was used as the starting point for the decision as to what is native and introduced in Missouri. Besides, Gleason (1968) explicitly omits Missouri from the list of states where this species has been found.

Viola arvensis Murray.

M 3863, North St. Louis Fr. Yd. (BN), 27 June 1974, one small colony. Determined by N. H. Russell and H. Scholz. Eurasia. *Viola arvensis* belongs to the group of plants which Steyermark (1963) excluded from his Flora as erroneously determined.

Oenothera heterophylla Spach subsp. **heterophylla.**

M 942, O'Fallon Fr. Yd. (TRRA, now dismantled), 16 June 1956, two large specimens, from which only parts were taken; *M 1018,* 14 July 1956, the same two plants. This species was annotated by W. Dietrich (University of Düsseldorf). It was previously determined as the native *O. rhombipetala* Nutt. According to Correll & Johnston (1970) a plant of eastern and north-central Texas and western Louisiana.

Plantago indica L. (*P. ramosa* (Gilib.) Aschers).

M 3977, Carrie Ave. Fr. Yd. (RI), 17 July 1976, one specimen. Determined by H. Scholz. Eurasia.

Lonicera maackii Maxim.

M 3985 (flowers) and *M 4001* (fruits) from the same plant (?), MP between Shaw Blvd. and Kingshighway Blvd., 14 Aug. 1976 and 18 Sept. 1976, one or several shrubs. *M 3997* (flowers) and *M 4004* (fruits), from the same shrub, 28 Aug. 1976 and 4 Oct. 1976, Inbound Fr. Yd. (RI, SL-SF, C&EI), one shrub. Determined by R. E. Weaver. Asia.

Symphoricarpos albus (L.) Blake.

M 3485, MP, between Tower Grove Ave. and Chouteau Ave., 8 Nov. 1970, one shrub. Determined by R. E. Weaver. North America, missing in Missouri.

Lactuca sativa L.

M 4002, Lesperance St. Fr. Yd. (MP), 18 Sept. 1976, one specimen. It lay uprooted on the ground, but it was seen in living condition on 28 Aug. when it was too juvenile for collecting. Determined by R. P. Wunderlin. Widely cultivated vegetable. Origin uncertain.

The following eight synanthropes were reported by Steyermark (1963) to occur in Missouri, but were not previously observed by me in the railroad network from 1954 through 1971 or were not surely recognized at that time.

Festuca ovina L.

M 2963, South 7th St. Fr. Station (MP), 21 July 1968, three specimens. Determined by R. W. Pohl. Eurasia.

Rorippa sylvestris (L.) Bess.

M 3822, dead end of the MP's Christy Lead, along Landsdowne Ave., 15 May 1973; *M 3832,* 30 June 1973, the same small colony. Determined by R. L. Stuckey. Eurasia.

Syringa vulgaris L.

M 3856, Pickrel Fr. Yd. (TRRA), 4 June 1974, one sterile shrub. Determined by R. E. Weaver. Europe.

Physalis ixocarpa Brotero.

M 2358 and *M 2388,* South Ranken Yd (TRRA), 14 June and 19 July 1964, in both cases one specimen (UMO). Determined by D. B. Dunn and W. G. D'Arcy. Southwestern U.S.A. and Mexico.

Physalis angulata L.

M 2493A, River Fr. Yd. (MRS), 10 July 1965,

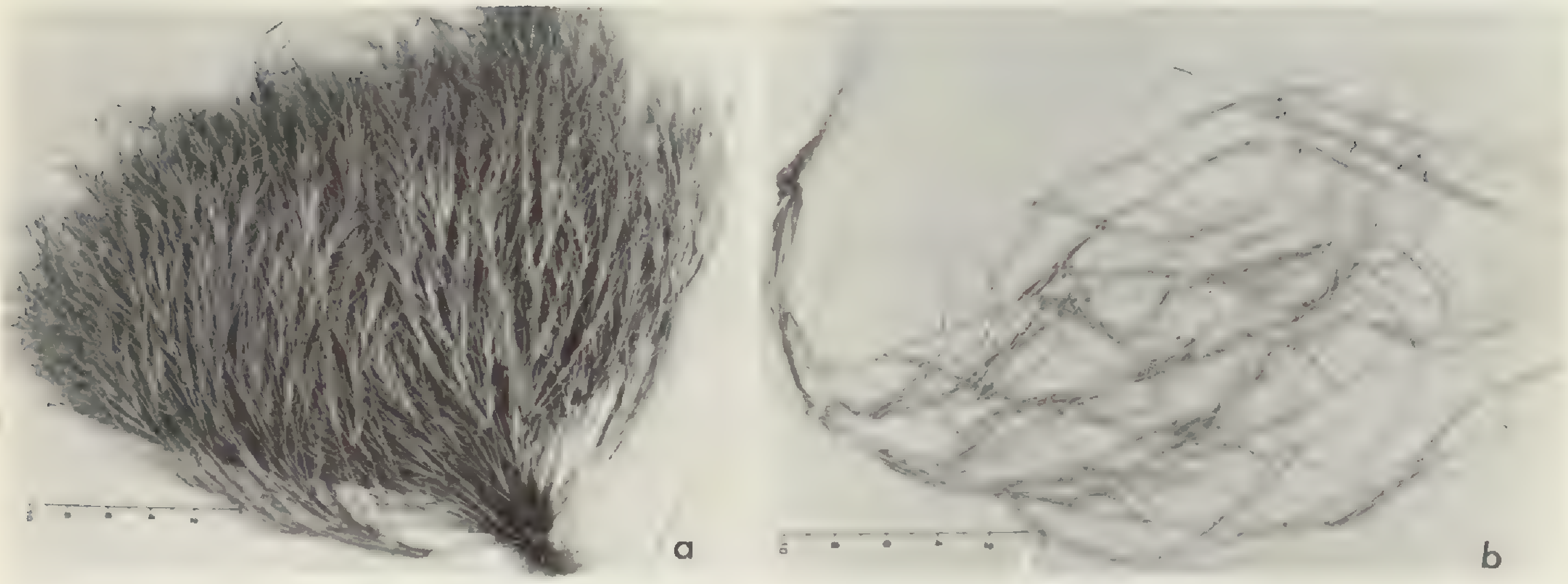

FIGURE 1. *Aristida oligantha* Michx.—a. Densely tufted, highly branched form (*Mühlenbach 4074,* MO).—b. Greenhouse-grown progeny of *Mühlenbach 4074* with normal growth form.

one specimen. Determined by W. G. D'Arcy. Southern U.S.A., West Indies, South America, Asia.

Tagetes erecta L.

M, Conrad & Conrad 3899, Baden Fr. Yd. (MKT), 6 Sept. 1975, one specimen. Determined by R. P. Wunderlin. Discovered by J. Conrad. Mexico.

Matricaria maritima L. var. *agrestis* (Knaf) Wilmott (*M. inodora* L.).

M 3891, North St. Louis Fr. Yd. (BN), southern reserve tracks of the grain elevator, 24 June 1975, one colony. Determined by R. P. Wunderlin. Europe.

Taraxacum laevigatum (Willd.) DC. (*T. erythrospermum* Andrz.).

M & Conrad 3916, Lesperance St. Fr. Yd. (MP), 1 Nov. 1975, one specimen. Determined by R. P. Wunderlin. As mentioned by me (Mühlenbach, 1979) a constant lookout for this species was carried out from 1956, but in vain. The first unicate was finally located in 1975. It was also the last one. It is odd indeed for on the streets of St. Louis *T. laevigatum* does not seem to be an extreme rarity.

The following species may also be added to the list of railroad synanthropes in St. Louis.

Cirsium undulatum (Nutt.) Spreng.

M 639, 18 June 1955; *M 1254,* 4 July 1957, Harlem Fr. Yd. (TRRA), one specimen. According to Steyermark (1963) it is rare in Missouri (five counties) and ranges from British Columbia to Arizona, east to Manitoba, North Dakota, Nebraska, Missouri and Oklahoma; in other words, it must be considered to be native. The same judgement on native status in Missouri and the general range of this species is given by Fernald (1950). But G. B. Ownbey, who annotated all my *Cirsium* collections, wrote to me on 9 December 1971: "You also have three additional American species: *C. discolor, C. altissimum* are native in your area, *C. undulatum* is adventive from the West, the Great Plains, to be exact."

The total number of species recorded from the railroads was 901, 414 being synanthropes and 487 native. About 20 additional species have withstood all efforts at determination. Some are too juvenile, some overripe, some damaged. Many of them are *Amaranthus* hybrids in different combinations. As previously, I have tried to avoid publication of uncertainly determined material.

Of the native species, one group merits a closer look, namely native Missouri plants that were collected in St. Louis County for the first time. (Steyermark (1963) combined the city of St. Louis with St. Louis County for this purpose, as do I.) Altogether there were 37 taxa (23 species, 14 intraspecific taxa) that were not previously reported from this area.

Most of them were seldom encountered, and they were usually not numerous. Likewise, the majority tend to be rare in Missouri. According to Steyermark (1963) eighteen of them were reported in five or fewer counties, six even being found only in one county. Twelve were known from six to twenty counties, and only seven were found in twenty-one and more counties. Stey-

ermark mentions further that among these thirty-seven taxa, eight grow along railroads. At least half of the thirty-seven were originally restricted to the western half of the state. Quite a few (seven) were known only from the southeastern lowlands (Missouri's Bootheel). It is of course of interest to learn the status of these plants. Are they autochthonic elements of St. Louis County's flora or have they been introduced by one means or another? It seems likely that the majority, even the great majority, have in fact been introduced. As mentioned, a majority of these plants were until recently only known from the western half of the state or from the Bootheel with no known intermediate stations. Only eight taxa were found in one or two of three counties (St. Charles, Franklin, Jefferson) bordering St. Louis County. Surely many of these native plants that appeared in St. Louis did not originate in Missouri itself but came from far away. It is easy to prove such assertions when varieties and forms are found that are missing in the native flora. Such observations have been made in Europe, but not in Missouri. From 1954 through 1971 the richest freight yards with rare synanthropes were Carrie Ave. (RI) and Baden (MKT). Of interest is the fact that half of the introduced natives were also found in both these yards. This is an additional indication that they are indeed introductions.

Five taxa were found along the so-called car cleanout tracks, where heavily polluted freight cars are swept and tidied up before loading. These tracks are now and then accompanied by piles of rubbish which, as they contain much combustible material, are occasionally set on fire. Finally the remainder is hauled away. It is astonishing to see that in spite of such harsh conditions many plants manage to survive. Such sites are the most promising places in the freight yards for discovering synanthropes. These tracks are quite confined in size and length and were visited and meticulously inspected at least three times in a season. In such places almost every plant, be it synanthrope or native, must be introduced by the railroad operations. It is almost inconceivable that these native plants had been overlooked for years before they were noticed.

Recently I became aware of a paper by Schultz (1976) on the synanthropic flora of the railroad system in Riga, Latvia. From Schultz's remarks and my own observations in St. Louis and Edmonton, Canada, it is quite evident that the role of refuse, dirt, and debris, which normally accompanies freight, is more important in the introduction of synanthropes than the role of the freight itself. This conclusion has apparently never been explicitly stated in the literature, but its importance is underscored by comparing the way refuse is handled in St. Louis and Riga compared with Edmonton. In the huge Calder Yard of the Canadian National Railways in Edmonton, freight cars are cleaned in an elaborate waste disposal system in which all solids are removed by washing or a vacuum system and taken away by truck to garbage dumps or an incinerator. In both St. Louis and Riga the cleaning system is much less elaborate, and solid refuse ends up on the car cleanout tracks and nearby areas. As a consequence, the car washing areas of the railroad yards in St. Louis and Riga were the richest sites for synanthropes, whereas very few synanthropes have ever been found in the vicinity of the Edmonton facilities.

The remainder of these thirty-seven native plants are most probably also introduced. Numerous observations in European yards have often demonstrated the introduction of native plants into them. One may even speak about secondary or even triple introduction, as for instance, when European plants naturalized in South Africa or Australia are reintroduced into Europe together with their native South African or Australian associates. One of the most frequently encountered plants of this group in Missouri, *Chenopodium desiccatum* var. *desiccatum*, has until now only been reported from one county, Jackson.

One other phenomenon should not be overlooked. As experience in Europe has taught, quite a few plants are able to spread spontaneously along trunk lines by ferroviatic migration from one station or yard to a neighboring one. Such evidence is missing in St. Louis. Eight taxa were indeed found on the right-of-way of different trunk lines or along some sidings, but only one of them was also found in a yard. They are all rarities. The participants of a ferroviatic migration usually show a distinct expansion along trunk lines, something which was totally missing in St. Louis.

The native introduced plants are the following:

Equisetum hyemale L. var. *pseudohyemale* (Farw.) Morton.

M 121, 5 June 1954, one colony that has shown intention to persist. This species was located later

in several other places. Determined by R. M. Tryon.

Typha angustifolia L.
M 2472, 31 May 1965, one large colony, persisting for many years. Another colony was later discovered, but not collected.

Muhlenbergia frondosa (Poir.) Fern. f. *commutata* (Scribn.) Fern.
M 2228, 21 Sept. 1963, one small colony. Determined by R. W. Pohl.

Brachiaria platyphylla (Griseb.) Nash.
M 2245, 29 Sept. 1963, two specimens. *M 3069,* 30 Oct. 1968, one large tuft. Determined by J. B. Van Schaack and R. W. Pohl.

Paspalum setaceum Michx.
M 3614, 12 July 1971, one colony. Determined by R. W. Pohl.

Cyperus odoratus L. (*C. ferax* L. C. Richard).
M 1862, 16 Sept. 1961, one specimen. *M 3427,* 13 Sept. 1970, scattered. Determined by R. Kral and T. M. Koyama.

Scirpus atrovirens Willd. var. *georgianus* (Harper) Fern.
M 3290, 9 June 1970, one dense colony or a huge tuft. Determined by T. M. Koyama.

Carex austrina (Small) Mackenz. (*C. muhlenbergii* Schkuhr var. *australis* Olney).
M 1755, 28 May 1961, one tuft (US). *M 2334,* 16 May 1964, one huge tuft. Determined by F. P. Hermann.

Tradescantia ohiensis Raf. × *T. virginiana* L.
M 1763, 30 May 1961, several specimens. Determined by E. Anderson.

Polygonum coccineum Muhl. var. *pratincola* (Greene) Stanford. *M 2984,* 15 Sept. 1968, one colony. Determined by H. A. Wahl.

Polygonum pennsylvanicum L. var. *laevigatum* Fern. f. *albineum* Farw.
M 2578, 9 Oct. 1965, one specimen. *M 2814,* 18 June 1967, one colony. Determined by H. A. Wahl.

Chenopodium desiccatum A. Nelson var. *desiccatum.*
M 1794, 1 July 1961, five specimens. Eleven collections followed. Eight of them came from the same yard. The impression is that this plant is quite widespread in St. Louis. It was known until now only from Jackson County. All determined by H. A. Wahl.

Chenopodium strictum Roth var. *glaucophyllum* (Aellen) Wahl.
M 1860C, 16 Sept. 1961, four specimens. *M 1884A,* 6 Oct. 1961. Determined by H. A. Wahl.

Mirabilis hirsuta (Pursh) MacM.
M 2373, 21 June 1964, one small colony (about eight specimens) (UMO). The plant grew on the same place the next year (*M 2458,* 22 May 1965), but then disappeared. Determined by D. B. Dunn.

Polanisia dodecandra (L.) DC. var. *trachysperma* (T. & G.) Iltis.
M 1807, 29 July 1961, two specimens. Determined by H. H. Iltis.

Draba reptans (Lam.) Fern. var. *micrantha* (Nutt.) Fern.
M 3498, 20 April 1971, one large colony. Determined by R. L. Stuckey.

Fragaria virginiana Duchesne var. *virginiana.*
M 3225, 25 April 1970, few specimens. Determined by F. G. Meyer.

Rubus frondosus Bigel. (*R. pennsilvanicus* Poir.).
M 3965, 5 July 1976, a small colony. Determined by R. E. Weaver.

Rosa arkansana Porter.
M & K. Kramer 556, 7 May 1955. Determined by W. H. Lewis.

Schrankia uncinata Willd. (*S. nuttallii* (DC.) Standl.).
M 2462, 22 May 1965, one specimen. Determined by D. Isely.

Lotus americanus (Nutt.) Bisch. (*L. purshianus* Clements & Clements).
M 1770, 17 June 1961, five or six sterile specimens (only one taken). *M 1789,* 1 July 1961, three specimens at the same place. Determined by J. D. Dwyer.

Psoralea tenuiflora Pursh var. *floribunda* (Nutt.) Rydb.
M 1945, 20 May 1962, one specimen. *M 1949,* 20 May 1962, one splendid specimen surrounded by many small sterile ones. Both collections gathered in the same freight yard. Determined by D. Isely.

Petalostemon multiflorum Nutt.
M 1978, 8 July 1962, one colony. Determined by L. H. Shinners.

Parthenocissus inserta (Kerner) K. Fritsch.
M 2930, 19 May 1968, one colony. Determined by K. R. Robertson.

Chaerophyllum tainturieri Hook.
M 1635, 11 June 1960, two specimens. Six further collections followed. This species is not a rarity in St. Louis. Determined by M. E. Mathias.

Spermolepis echinata (Nutt.) Heller.
M 1729, 13 May 1961, one colony, observed on the same spot several times later, also in 1962. Determined by M. E. Mathias.

Ptilimnium capillaceum (Michx.) Raf.
M & White 4045, 23 July 1977, two dwarf specimens. Determined by M. E. Mathias.

Monarda punctata L.
M 1785, 25 June 1961, few specimens. *M 3938,* 12 June 1976, one specimen. Determined by J. A. Steyermark and A. G. Jones.

Penstemon tubaeflorus Nutt.
M 2098, 2 June 1963, one small colony. Determined by A. G. Jones.

Solanum carolinense L. f. *albiflorum* Benke.
M 3086, 4 June 1969, five specimens. *M 3089,* 4 June 1969. In two different places.

Astranthium integrifolium (Michx.) Nutt.
M 1822, 19 Aug. 1961, one specimen. Determined by W. H. Lewis.

Aster parviceps (Burgess) Mackenz. & Bush.
M 2262, 6 Oct. 1963, one small colony or a large tuft, also *M 2305,* 26 Oct. 1963. Determined by R. P. Wunderlin.

Aster dumosus L.
M 2568, 30 Oct. 1965, one huge specimen. More flowers than leaves, a "white cloud" indeed. Determined by R. P. Wunderlin.

Rudbeckia amplexicaulis Vahl (*Dracopsis amplexicaulis* (Vahl) Cass.).
M 2111, 22 June 1963, one specimen. *M 3938,* 12 June 1976, one specimen. Determined by R. P. Wunderlin.

Echinacea angustifolia L.
M 2119, 25 June 1963, one specimen. Determined by R. P. Wunderlin.

Helianthus rigidus (Cass.) Desf. ssp. *subrhomboides* Heiser (*H. laetiflorus* Pers. var. *rigidus* (Cass.) Fern.).
M 2745, 9 Oct. 1966, one colony. Determined by C. B. Heiser, Jr.

Aster pilosus Willd. var. *pringlei* (Gray) Blake.
M 2769, 30 Oct. 1966, few specimens. Determined by R. P. Wunderlin. This taxon can even be considered as a novelty for Missouri, because it was excluded in Steyermark (1963) as erroneously determined.

Finally three species will be mentioned that were not found along the railroads, but that are all very rare synanthropes, previously observed in Missouri in only one or two counties of Missouri outside St. Louis.

Stellaria graminea L.
M 3929, 6 June 1976, lawn along the house, 5201 Landsdowne Ave., one very dense colony persisting in the following years. The residents of this house were unable to explain how this plant could have arrived here. Determined by J. McNeil. Eurasia.

Papaver somniferum L.
M 1667, 16 July 1960, between the sidewalk and the house, 6422 N. Broadway, one specimen. Unknown in the wild, probably originating in the Mediterranean region.

Coronopus didymus (L.) Sm.
M 3851, 1 June 1974, in the backyard of my house, 4984 Neosho St., one colony, persisting there up to now. Determined by R. L. Stuckey. Europe. I suspect that this synanthropic plant has been "introduced" by me, like a number of plants mentioned earlier (Mühlenbach, 1979: 101). They suddenly appeared on my property one after another. They are all frequent plants on the railroads in St. Louis. For this reason I consider them as introductions from the railroads to my backyard. The seeds were picked up accidently during my excursions by my clothing and later stripped off. Especially the cuffs of my trousers were frequently full of seeds of different plants. Unfortunately, I have never seen *Coronopus didymus* on the railroads. However, this plant is very inconspicuous and might have been overlooked. One more new introduction, *Eupatorium rugosum* Houtt., was discovered in my backyard in 1979. It is common along the railroads. The last arrival was *Carduus nutans* L. In this case I do not blame the railroads. Most probably the seed was transported by wind from some vacant lot in the city where this plant has spread considerably in the last few decades.

It is also worthwhile to mention a weed that unexpectedly appeared in the Missouri Botanical Garden. *Chenopodium ficifolium* Sm. was discovered by the Director of the Kew Royal Botanic Garden, J. P. M. Brenan, on his visit to the Missouri Botanical Garden, on the lot behind the newly erected Lehmann Building (*W. G. D'Arcy 5963*, 27 June 1972). *Chenopodium ficifolium* was found at several other places in the Garden in the later years. It was last observed in 1976.

Finally, a most unusual collection of *Aristida* (*M 4074*, former RI, SL-SF and C&EI, Inbound Fr. Yd., 22 Oct. 1977) may be mentioned. It was originally collected as a unicate in a normal population of *A. oligantha* Michx. As illustrated in Figure 1a, which represents only one-third of the plant, it was extremely densely tufted and highly branched. The size of the spikelet parts were as follows: lower glume 0.9–1.2 cm long including the awn 0.1–0.2 mm long, 5–7-nerved, upper glume 1.4–1.6 cm long including the awn 0.4–0.5 mm long; lemma 1.1–1.6 cm long, the central awns 1.6–1.8 cm long, the lateral awns 1.3–1.8 cm long. This specimen seems not to have an exact parallel with any described species in this large genus. A number of prominent agrostologists studied it but were unable to name it. It was, however, generally thought to be closely related to *A. oligantha* Michx., a species with glumes (1.5–)2–3 cm long, the lower 3–5-nerved, the lemma (1.5–)1.8–2.2 cm long and the awns (2–)4–7 cm long. Subsequently seeds of *M 4074* were grown (by Dr. P. Hoch) in the greenhouse. Progeny fell within the normal range of *A. oligantha*. The branching was much less dense (Fig. 1b), and spikelet parts range as follows: lower glume 1.8–2.0 cm long, 5-nerved, upper glume 2.0–2.4 cm long, lemma 1.4–1.5 cm long, awns 3.7–4.3 cm long. The unusual plant may well represent an extreme recombinant or a mutant, although unusual growth effects due to chemicals in its environment cannot be completely disregarded.

It is clear beyond any doubt that modern weed killing exerts a disastrous effect on the railroad vegetation. It was of special interest to observe that in spite of this the vegetation may quite rapidly reappear when the herbicide spraying is suddenly discontinued. This was observed in both Ranken yards (TRRA). These yards were used as holding yards for passenger trains. As the number of these trains constantly dwindled, the yards were abandoned and later dismantled. Of course, herbicide spraying was discontinued. A nice vegetation reappeared, demonstrating at the same time the phenomenon of trivialization, the process whereby native species take over synanthropes.

But events of another kind took place in another yard, namely, Carrie Ave. freight yard (RI). This yard had the highest yield of rare synanthropes (Mühlenbach, 1979: 92). Here, as everywhere, the effects of weed killing increased each year. But in 1974 weed killing was suddenly stopped for two years, while the railroad company continued normal operations, contrary to the situation in the Ranken yards. When I visited Carrie Ave. again in 1976, a luxurious vegetation had reappeared with a splendid display of synanthropic plants, reminiscent of bygone times 20 years ago. Even two Missouri novelties were discovered (*Reseda lutea* and *Plantago indica*, as unicates). One frequently hears about vanishing prairie, rain forests, and so on, but the same thing is now happening to the railroad flora in St. Louis and, of course, everywhere else as well. Only very few have realized that.

Later in 1976 the freight yard was thoroughly sprayed with herbicides and the whole splendor was annihilated. In the autumn this yard looked like all other freight yards in St. Louis, a desolate, sterile landscape. I revisited it again in 1980, and to my surprise the vegetation was flourishing again, but no rarities could be detected. As it turned out, this freight yard was taken over by another railroad company (St. Louis and Southwestern Railway or Cotton Belt Route), which stopped all regular activities in the yard. Only one track was kept in operation for through-trains of other companies. As a consequence, the vegetation was thoroughly trivial.

On the basis of these observations, it is possible to enumerate a rule concerning the weed killing process. If herbicide spraying in a yard is discontinued, vegetation will promptly reappear. In case the usual operations of a yard are not continued, trivialization will follow, but when normal operations of a yard are continued, synanthropes appear. How many and which kind will depend on the volume and character of the cargo. But natives may also appear for the first time. My conviction that native plants are also spread by railroads was strengthened by finding *Rudbeckia amplexicaulis* Vahl in 1976. It is a very conspicuous plant and it is inconceivable that I had overlooked it for 22 years.

As in other botanical endeavors, railroad

botany published determinations of synanthropes must occasionally be changed. In Mühlenbach (1979) *Kochia iranica* (Hausskn. & Bornm.) Litw. turned out to be *K. sieversiana* (Poll.) C. A. Mey. according to W. A. Weber. *Kochia sieversiana* has been found repeatedly in Missouri, but in only one place, Stockyard Switch, Joplin, Jasper County. *Centaurea stoebe* L. subsp. *stoebe* and *C. maculosa* Lam. in Mühlenbach (1979) turned out to be the same species. According to G. Wagenitz (Göttingen), who has determined my *Centaurea* material, plants of the *C. stoebe* group are not rare in North America, but have mostly been determined as *C. maculosa*.

A mistake in the citation for Sauer (1967) was also made in Mühlenbach (1979) and is here corrected.

R. L. Stuckey has kindly pointed out to me that there is an older American paper (Stair, 1900) on railroad weeds, that was overlooked by me earlier. Besides this he mentioned two other more recent papers (Catling & McKay, 1974; Thompson & Heineke, 1977) not cited by me. An additional paper that has recently been published is Arnold (1981).

Mrs. Jean Warholic (Freeville, N. Y.) brought to my attention Ross (1943). This paper treats the weeds at the Knapp farm of George Peabody College for Teachers in 1923. Among other things, the plants on the right-of-way of the Nashville, Chattanooga & St. Louis Railroad that transverses the farm were enumerated and evaluated—altogether 82 species. The great majority were also found in St. Louis.

It also seems worthwhile to mention here a corrected determination for *Arctium tomentosum* Mill., mentioned as a synanthropic species in Steyermark (1963). Both collections at MO are not *A. tomentosum* but *A. minus* (Hill.) Bernh.

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REVISION OF THE GENUS *STERIGMAPETALUM* (RHIZOPHORACEAE)

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ABSTRACT

The genus *Sterigmapetalum* consists of 7 species, with 4 newly described species (*S. exappendiculatum, S. heterodoxum, S. resinosum,* and *S. tachirense*), and 1 new subspecies (*S. guianense* subsp. *ichunense*). On the basis of the presence or absence of a resinous exudate, development or reduction of lateral flanges of the petals, and opposite or verticillate leaves, two subgenera are recognized: *Sterigmapetalum* and *Balsamocaulon.* On the basis of their hypogynous flowers and superior ovaries, *Cassipourea* and *Sterigmapetalum* are placed in a new tribe, Hypogyneae, within the Rhizophoraceae. A key to the species is provided, followed by a description of the species and their geographical distribution. Newly discovered anatomical evidence, which reveals the presence of a P-type sieve element in the Rhizophoraceae, indicates that the family should be excluded from the Myrtales and is additional evidence supporting the view provided by the gross morphological floral details that the family is atypical in the Myrtales, and should be removed from that order.

Sterigmapetalum was established in 1925 by Kuhlmann with a single species, *S. obovatum,* collected from Amazonian Brazil. It was differentiated from what was considered a related genus, *Blepharistemma* Wall. ex Benth., by the possession of dioecious flowers, of calyx segments and stamens, absence of a disc, and a greater number of cells of the ovary. Since that time, two additional species, *S. colombianum* Monachino (1944) from Colombia, and *S. guianense* Steyermark (1952) from the Venezuelan Guayana, have been published.

During recent explorations in Venezuela near the Colombian border, a fourth species has been discovered. In an attempt to bring our present knowledge of the genus up-to-date, material has been borrowed from the herbaria of F, NY, and US. Unfortunately, the dioecious character of the genus, together with the paucity of specimens available in herbaria, have added to the difficulties of revision. However, as a result of this study, additional taxa have become manifest and are described below. We wish to thank the curators of the aforementioned herbaria for the loan of their material.

GROSS MORPHOLOGY

A resinous exudate covers the young buds, peduncles, and upper internodes of the stem in *S. heterodoxum* and *S. exappendiculatum,* but is not found among other members of the genus. This character, associated with the reduced lateral flanges of the petals, and opposite leaves, form the basis for the establishment of a subgeneric category within the genus.

Stipules. The stipules are uniformly interpetiolar throughout the taxa. They are glabrous in *S. colombianum, S. tachirense, S. heterodoxum,* and *S. exappendiculatum.* In *S. obovatum* and *S. guianense* a more or less persistent, densely sericeous indument covers the external surface.

Leaves. The leaves are usually 3–4-verticillate, but in *S. heterodoxum* and *S. exappendiculatum* of subgenus *Balsamocaulon* they are always opposite. Occasional terminal leaves of *S. tachirense,* a taxon with ordinarily 3-verticillate leaves, may be opposite. The leaf blades are mainly cuneate at the base and broadest above the middle, resulting usually in an obovate shape. In *S. tachirense* they are rounded or broadened at the base. In *S. exappendiculatum* they are elliptic-oblong and broadest toward the middle. The leaf margins are mainly entire, but show varying degrees of crenulation, rather markedly so in *S. exappendiculatum.*

Inflorescence. The inflorescence is usually subterminal and arises in the axils of the uppermost leaves. Two or more peduncles near the apex of the stem in the axils of the uppermost leaves are present in several species, but in *S. heterodoxum* and *S. exappendiculatum* of subgenus *Balsamocaulon* the peduncles arise lower on the stem between the second and sixth internodes below the apex, and are solitary in the leaf axils. The

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flowers are arranged in unbranched or 1–4-branched dichotomous cymes, and are sessile to shortly pedicellate. In subgenus *Balsamocaulon* the peduncles are covered with a resinous exudate, especially near the apex.

Calyx. The calyx is valvately 4–7-toothed. *Sterigmapetalum tachirense* is the only species thus far known in the genus with four calyx lobes. The calyx tube encloses the floral parts, but is hypogynous and not coherent either with the ovary or other parts of the flower. The outer surface varies from glabrous to densely sericeous. In subgenus *Balsamocaulon* a resinous exudate covers the young calyx and margins of the lobes, which are manifestly elevated into thickened, linear ridges. The inner surface of the calyx lobes is usually densely strigose or sericeous.

Petals. The petals are free and hypogynous, inserted at the base of the flower between the base of the calyx tube and the disclike membrane to which the stamens are attached (Fig. 1A). They vary in number from four to six and differ greatly in ornamentation (Fig. 2). In shape they vary from linear, oblanceolate, to panduriform, with a usually 3-lobed or 3-parted apex and two lateral flanges or lobes bearing 2–18 short to elongated, fimbriate, often curling appendages (Fig. 1A). Between the lateral flanges is a central, hooded, incurved portion with three to many crowded, involute appendages. This central apical part is often surmounted by a penicillate tuft of hairs, which are also inflexed. Hairs may also be present on the dorsal part of the petal, and occasionally elsewhere. Sometimes, as in *S. exappendiculatum,* the apical tuft of hairs, as well as the fimbrillate lateral flanges, are lacking (Fig. 2: 2A, 2B).

Androecium. The stamens vary in number from 8 to 12 in the staminate flowers, and are usually unequal in an alternating arrangement (Fig. 1C). The anthers are versatile, dorsifixed, broadly oblong, and rounded at both ends. The filaments are attached to the border of an annular membranous structure, which has been referred to as a disc (Fig. 1C). This structure could be equally interpreted as the fused bases of the filaments. It is inserted at the base of the flowers between the base of the petals and the ovary or ovary rudiment.

Gynoecium. The ovary is completely superior in the pistillate flower (Fig. 1A), as is the ovary rudiment in the staminate flower (Fig. 1B). Both are inserted on the receptacle at the base of the flower. The ovary is depressed-globose to subobovate, and 5–6-locular with two pendulous ovules in each cell. In the few species in which pistillate flowers are known, it is covered by a dense tomentum. The style is very short or obsolete. The very short stylar branches are covered by a crowded mass of incurved stigmatic threads, which form a radiate structure depressed centrally. At the base of the ovary but not adherent to it is the disc. In the pistillate flowers, minute projecting staminodia, usually 10–12 in number, are attached to the border of the disc (Fig. 1B).

Anatomical features. As a result of his recent studies of sieve-element plastids in various families usually included within the Myrtales, Behnke (1983) found the so-called (S-type) plastid, those containing several spherical starch grains, to be characteristic and constant within the order. Of great significance is his discovery that the sieve-element plastids of the Rhizophoraceae are completely unlike those of any of the other families of the Myrtales in lacking starch, but instead contain numerous protein crystals, for which reason these plastids are placed in the P-type group. Although the genera *Sterigmapetalum* and *Cassipourea* were not studied by him, four other genera (*Rhizophora, Bruguiera, Carallia,* and *Crossostylis*) were investigated.

GENERIC AFFINITIES

The genus *Sterigmapetalum* is closely related to *Cassipourea* Aubl. Both genera have superior ovaries, in which respect they are at variance with the other genera placed within the family Rhizophoraceae. In a revision of the Amazonian species of the family, Prance et al. (1975) differentiated these two genera on the basis of verticillate (*Sterigmapetalum*) vs. opposite (*Cassipourea*) leaves, laciniate petals (*Sterigmapetalum*) vs. spatulate petals with appendages (*Cassipourea*), and pedunculate inflorescences (*Sterigmapetalum*) as opposed to sessile, axillary ones (*Cassipourea*). In light of our present knowledge, it should be modified to state that the petals of *Sterigmapetalum* usually have two lateral flanges, each with 2–18, short to elongated, fimbrillate appendages, borne on either side of an incurved or inflexed, central lobe furnished either with a dense tuft of hairs or with three appendages.

When Kuhlmann described *Sterigmapetalum* (1925), he stated that the genus, as then known only from Brazil, comprised very tall trees inhabiting high land, whereas *Cassipourea* was considered to be a genus of small trees. However,

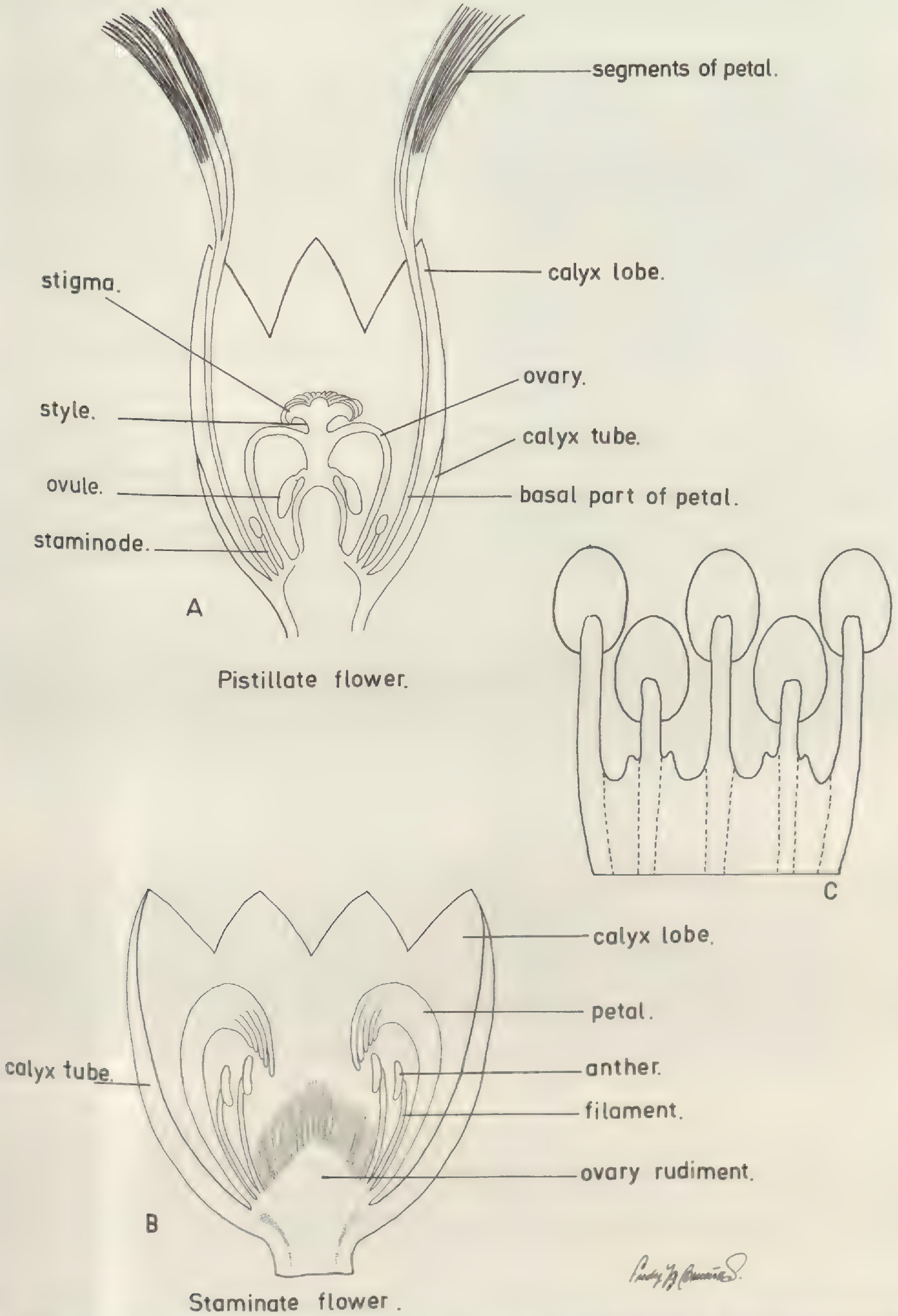

FIGURE 1. A. *Sterigmapetalum obovatum*, pistillate flower, semi-diagrammatic. B. *Sterigmapetalum guianense*, staminate flower, semi-diagrammatic. C. Portion of androecium with annular disk, showing alternating longer and shorter filaments, *Sterigmapetalum guianense*.

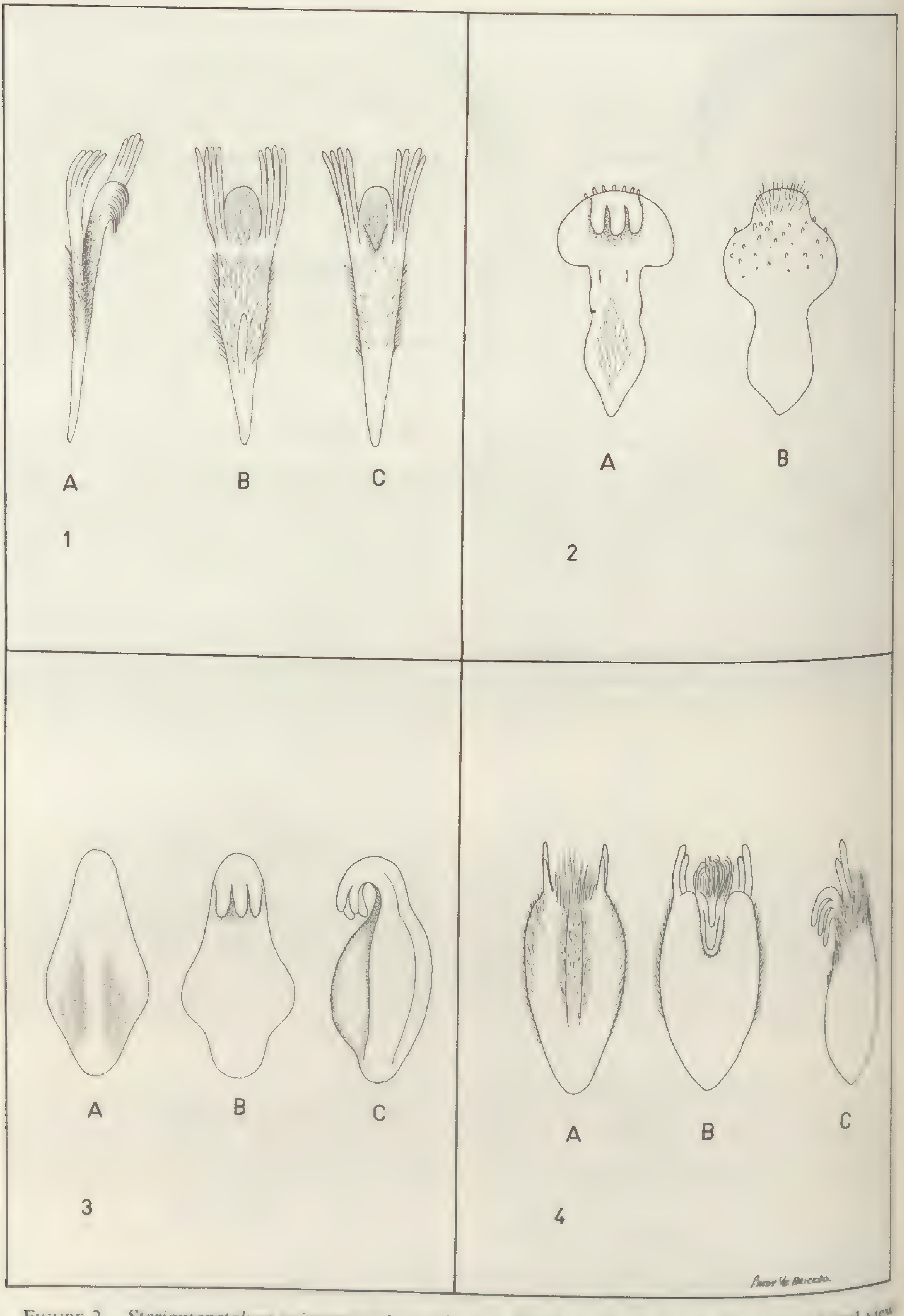

FIGURE 2. *Sterigmapetalum guianense* subsp. *ichunense*. 1A. Petal, lateral view; 1B. Petal, dorsal view; 1C. Petal, ventral view. *Sterigmapetalum exappendiculatum*. 2A. Petal, ventral view; 2B. Petal, dorsal view. *Sterigmapetalum resinosum*. 3A. Petal, dorsal view; 3B. Petal, ventral view; 3C. Petal, lateral view. *Sterigmapetalum heterodoxum*. 4A. Petal, dorsal view; 4B. Petal, ventral view; 4C. Petal, lateral view.

this latter observation does not stand the test of observations made on *Cassipourea* in other countries. In Panama, for example, Croat (1978) reported *Cassipourea elliptica* as a tree "13–17 m tall," and refers to a report by Allen to a tree as much as "30 m" tall. In Venezuela *Cassipourea* may vary from a shrub only 1.8–4 m tall to trees 8–15 m in height.

As a result of a study of these two genera, we find that the chief differences existing between them may be summarized in Table 1.

TABLE 1. Comparison of *Sterigmapetalum* and *Cassipourea*.

Sterigmapetalum	*Cassipourea*
Flowers dioecious.	Flowers perfect.
Style absent with sessile large stigma.	Style elongated and exserted.
Stamens included.	Stamens at least equaling calyx and slightly exserted.
Stamens 8–12.	Stamens 20–25.
Inflorescence pedunculate.	Inflorescence sessile.
Appendages of lateral flanges glabrous.	Appendages of petals pilosulous.
Lateral flanges of petals with 2–18 appendages.	Lateral flanges of petals with numerous appendages.
Petals with 2 lateral flanges (lobes) and a central incurved lobe.	Petals simple, not lobed.
Ovary 5–6-celled.	Ovary 2–4-(usually 3)-celled.
Leaves 3–4-verticillate, more rarely opposite.	Leaves opposite.

TAXONOMIC POSITION

Since both *Sterigmapetalum* and *Cassipourea* have hypogynous flowers, it is instructive to note how previous workers have characterized the family Rhizophoraceae in their respective treatments. At the time Kuhlmann (1925) published *Sterigmapetalum,* he considered it closest to the genus *Blepharistemma,* as a member of the tribe **Macariseae**, which, according to Schimper (1893), consisted of genera with perigynous flowers. Melchior (1964) placed the Rhizophoraceae within the Myrtales (Myrtiflorae), among mostly epigynous, rarely perigynous families. The Rhizophoraceae were described as having the ovary more or less united with the floral axis.

Bentham and Hooker (1862) divided the Rhizophoraceae (by them designated Rhizophoreae) into three tribes. The genera *Cassipourea, Blepharistemma* of the West Indies, and *Dactylopetalum* of Africa and Madagascar, were placed in the tribe Legnotideae and separated from other genera of that tribe by their superior ovary. Engler (1876) characterized the Rhizophoraceae as having an ovary "*saepissime infero, raro supero,*" and *Cassipourea* is described as having the ovary "liberum." Schimper (1893) recognized two subfamilies of the Rhizophoraceae: (1) **Rhizophoroideae** and (2) **Anisophylloideae**, the former distinguished by stipulate, opposite leaves, epigynous or perigynous flowers, single style, endosperm present, and the fruit a berry or capsule, while the latter was differentiated on the basis of exstipulate, alternate leaves, epigynous flowers, three or four styles, absence of endosperm, and the fruit a drupe, or dry and indehiscent. Moreover, within the subfamily **Rhizophoroideae** two tribes were elaborated: (1) **Gynotrocheae** with epigynous flowers, seed without appendages, leaf blades with calcium oxalate crystals, and placenta continuous with the style, and (2) **Macariseae** with perigynous flowers, seed with appendages, simple crystals together with pairs of calcium oxalate in the leaf blades, and the placenta discontinuous with the style.

This treatment was modified by Melchior (1964) by treating the above categories as four equal tribes: (1) **Macariseae**, (2) **Gynotrocheae**, (3) **Anisophylleae**, and (4) **Rhizophoreae**, the first two characterized by the possession of stipulate opposite leaves, one style, and endosperm, the **Anisophylleae** by its exstipulate leaves, three to five styles, and no endosperm, and the **Rhizophoreae** by being mangrove plants with seeds producing an elongated protruding hypocotyl that germinates within the fruit; the other tribes consist of inland plants whose seeds germinate in the soil outside the fruit.

Many authors have characterized the Rhizophoraceae as having perigynous or epigynous flowers with the ovary stated to be mostly inferior. Lawrence (1963) described the stamens as "situated on the outer edge of a lobed perigynous or epigynous disk," but further characterized the family as having the "ovary variable in position depending on degree of adnation of perianth (i.e., superior, half inferior, or incompletely inferior)," while Standley and Williams (1962) described the ovary as "usually inferior," but also stated

that the "calyx-tube is more or less adnate to the ovary, rarely free, the limb produced beyond the ovary," but, in their description of the genus *Cassipourea* indicated the ovary as free. Heywood (1978) stated that the flowers are "hypogynous to epigynous," and the ovary "inferior or superior." Aristeguieta (1973) described the ovary as varying from superior to semi-inferior, and correctly characterized *Sterigmapetalum* and *Cassipourea* as genera having superior ovaries. Croat (1978), likewise, correctly stated that the ovary is superior in *Cassipourea,* as did Jonker (1942). In his description of the family Rhizophoraceae Hutchinson (1959) stated that the calyx tube is "adnate to the ovary or free."

Cronquist (1968) placed the Rhizophoraceae in the order Cornales, characterized by him partly as having epigynous flowers and indehiscent fleshy fruits. He also considered that its possession of well-developed endosperm and unitegmic ovules was consistent with its inclusion as a family within the Cornales. At that time he believed it to be "most useful to include the Rhizophoraceae in the Cornales as a near-basal side-branch not far distant from the Myrtales. If one prefers small orders and does not object to monotypes, the establishment of a separate order might perhaps be defended."

This concept of a distinct order for the Rhizophoraceae was subsequently defended by Cronquist (1981: 655–659). In this latest work (Cronquist, 1981), he recognized the family as a monotypic, separate order, Rhizophorales, which he placed between the Myrtales and Cornales. Principally on the basis of its absence of internal phloem, he separated the Rhizophorales from the Myrtales, while from the Cornales the separation is based mainly on the possession of bitegmic instead of unitegmic ovules, although he previously (Cronquist, 1968) stated that unitegmic ovules were common to both Rhizophoraceae and Cornales, as well as by additional characters of stipulate leaves and absence of iridoid compounds.

The flowers of the Rhizophoraceae are stated by Cronquist (1981) to be perigynous or epigynous, but he mentioned the genera *Cassipourea* and *Macarisia* as having perigynous flowers with a superior ovary. Actually, Cronquist (1981) expressed uncertainty in the proper disposition of the Rhizophoraceae, and suggested various possibilities for its placement, not only in the Cornales and Myrtales, both of which he believed unjustified, but also in the order Rosales. The latter order he considered as having characters too primitive to encompass the Rhizophoraceae, although he suggested that affinities with the Grossulariaceae and Hydrangeaceae might be conceivable. Since the Rhizophoraceae are not compatible with any of these three orders, Cronquist's alternative was to treat the family as a distinct, monotypic order.

Recent anatomical investigations on the plastids of sieve elements support the view that the Rhizophoraceae should be excluded from the Myrtales. The previous work on nearly 400 families of flowering plants by different workers (Behnke, 1974, 1976, 1981a, 1981b, 1982a, 1982b; Behnke & Pop, 1981; Dahlgren, 1980; Dahlgren & Thorne, 1983; Mabry, 1977) have shown that the plastids of the sieve element may be referred to either the S-type with starch grains or the P-type with protein crystals. Based on P-type plastids in the Rhizophoraceae, as contrasted with S-type in other families of the Myrtales (Melastomataceae, Crypteroniaceae, Penaeaceae, Oliniaceae, Combretaceae, Lythraceae, Sonneratiaceae, Punicaceae, Myrtaceae, Trapaceae, and Onagraceae), Behnke (1982b) suggested that the Rhizophoraceae be excluded from the Myrtales.

These new anatomical data provide further evidence to support the previously noted trend in the family from hypogyny to epigyny, and especially the atypical condition of *Sterigmapetalum* and *Cassipourea,* as being inconsistent with other members of the Rhizophoraceae and families of the Myrtales. The combination of anatomical evidence with that of the divergent floral structures of the Rhizophoraceae may well justify the exclusion of the family from the Myrtales, and claim for it a new position within an alliance of families having P-type plastids and compatible floral features.

TAXONOMY

Since both *Sterigmapetalum* and *Cassipourea* have hypogynous flowers with completely superior ovaries that are not united to the floral axis (Fig. 1A, B), they may be considered here as constituting a new tribe within the family, described as follows:

TRIBE **HYPOGYNEAE** Steyermark & Liesner. Type: *Cassipourea* Aubl., Fl. Guiane 1: 529, *t. 211.* 1775.

Flores hypogyni. Folia opposita vel verticillata. Ovarium superum.

Sterigmapetalum Kuhlmann, Arch. Jard. Bot. Rio de Janeiro 4: 359. *t. 32.* 1925. TYPE: *Sterigmapetalum obovatum* Kuhlmann; Aristeguieta, Fam. Gen. Arb. Ven. 605. 1973; Albuquerque in Prance et al., Acta Amaz. 5: 13. 1975.

Trees with interpetiolar stipules. Leaves opposite or 3–4-verticillate, petiolate, entire or crenulate-serrulate. Inflorescence axillary, subterminal or in the upper axils, pedunculate, cymose, the cymes congested, unbranched or dichotomously 1–4-branched. Flowers unisexual (the plants dioecious), actinomorphic, few to numerous, sessile or pedicellate. Calyx campanulate, 4–7-dentate or -lobed, the teeth or lobes valvate. Petals usually of the same number as the calyx lobes, 4–6, free, hypogynous, inserted between the base of the calyx tube and the base of the staminal membrane, linear, oblanceolate or panduriform, 3-lobed or 3-parted at the apex with 2 lateral flanges bearing 2–18, short to elongated, fimbrillate appendages on either side of a central, hooded, inflexed portion bearing 3 to many crowded, incurved appendages, this central portion often surmounted by an inflexed penicillate pubescent tuft. Stamens 8–12, usually unequal. Anthers versatile, dorsifixed, broadly oblong, rounded at the base and apex. Filaments attached to the border of or fused with a basal annular membrane which is hypogynously inserted at the base of the flower. Ovary rudiment present in the staminate flowers. Ovary superior, depressed-globose to subobovate, 5–6-locular, each cell 2-ovulate; ovules pendulous. Style very short or obsolete, the very short stylar branches covered by a crowded mass of incurved stigmatic threads. Fruit a septicidal, 5–6-celled capsule; seeds collateral, pendulous, oblong, winged; wings oblong-falciform, appendiculate or elongated, caducous. Endosperm oleaginous, slightly thick; radicle cylindrical; cotyledons foliaceous, flat, about equaling the length of the radicle.

Geographical distribution: Seven species are known, distributed in Amazonian Brazil north to the Guianas, Venezuela, and eastern Colombia (Fig. 3).

The genus *Sterigmapetalum* may be divided into two subgenera:

1a. No resinous exudate present; leaves usually 3–4-verticillate, rarely opposite; lateral flanges of the petals well developed with several to many fimbrillate appendages .... Subgenus *Sterigmapetalum*

1b. Resinous exudate present on young buds, peduncles, and upper cauline axis; leaves opposite; lateral flanges of the petals reduced to nearly obsolete .... Subgenus *Balsamocaulon*

KEY TO THE SUBGENERA AND SPECIES OF *STERIGMAPETALUM*

1a. Leaves always opposite; resinous exudate present on apical portion of stem, peduncle, and buds; peduncle solitary, axillary between the 2nd and 6th nodes below the apex of the stem .... Subgenus *Balsamocaulon*

- 2a. Leaves acute or subacute and narrowed at the apex, broadest at the middle; stipules acute to acuminate; petals lacking lateral flanges, glabrous .... 6. *S. resinosum*
- 2b. Leaves truncate to rounded at the summit, broadest above the middle; stipules obtuse; petals with 2 lateral flanges, ciliate, apically densely pilose .... 7. *S. heterodoxum*

1b. Leaves mainly 3–4-verticillate, rarely opposite; resinous exudate absent; peduncles at or just below apex of stem .... Subgenus *Sterigmapetalum*

- 3a. Leaves rounded at the base; staminate flowers 4-merous .... 5. *S. tachirense*
- 3b. Leaves mainly cuneate, acute or subobtuse at the base; staminate or pistillate flowers 5–6-merous, rarely 7-merous.
  - 4a. Peduncles 3–7 cm long; inflorescence manifestly 2–4-dichotomously branched; lateral flanges of the petals 14–21 mm long including the appendages greatly exceeding the calyx tube, 14–21 mm long .... 1. *S. obovatum*
  - 4b. Peduncles 0.3–3 cm long; inflorescence either 1-dichotomous or with fasciculately crowded flowers terminating the axes; lateral flanges of the petals, including the appendages, at most 6 mm long, scarcely equaling or only slightly exceeding the calyx tube.
    - 5a. Leaves broadest at the middle, narrowed above the middle to the apex; leaf margins more or less denticulate-crenulate; petals lacking fimbrillate lateral flanges .... 3. *S. exappendiculatum*
    - 5b. Leaves broadest above the middle, truncate-rounded or emarginate at the apex; leaf margins entire; petals with fimbrillate lateral flanges.
      - 6a. Upper leaf surface with conspicuously elevated tertiary venation.

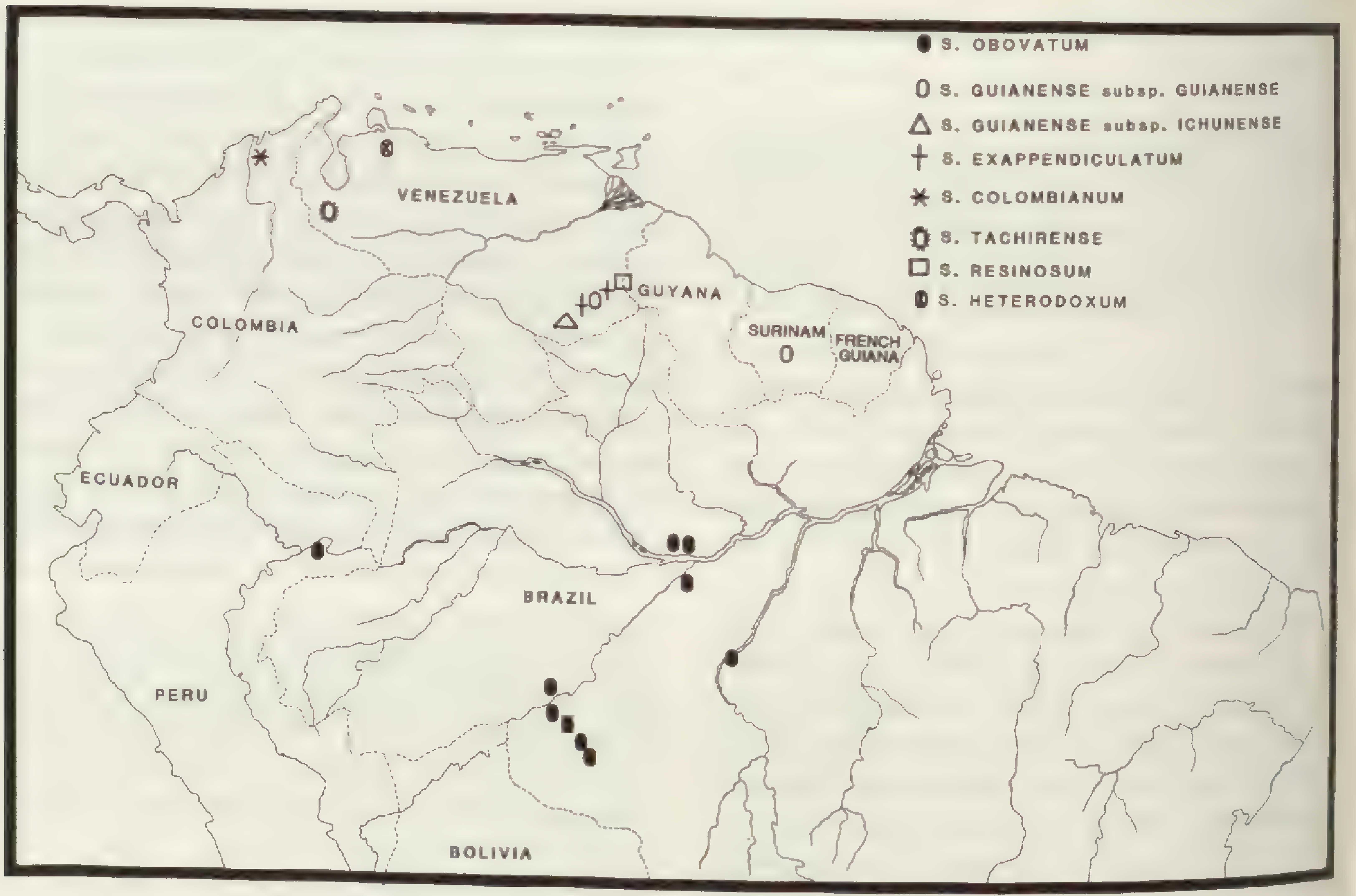

FIGURE 3. Geographical distribution of the genus *Sterigmapetalum.*

7a. Stipules glabrous without; calyx exterior glabrous or at most sparsely appressed-pubescent .... 4. *S. colombianum*
7b. Stipules densely pubescent without; calyx exterior densely sericeous .... 2a. *S. guianense* subsp. *guianense*
6b. Upper leaf surface lacking elevated tertiary venation .... 2b. *S. guianense* subsp. *ichunense*

Sterigmapetalum subgenus **Sterigmapetalum**. TYPE: *Sterigmapetalum obovatum* Kuhlmann.

Exsudatum resinosum nullum. Folia vulgo 3–4-verticillata, raro opposita. Extensiones laterales petalorum bene evolutae cum appendicibus fimbriatis.

1. **Sterigmapetalum obovatum** Kuhlmann, Arch. Jard. Bot. Rio de Janeiro 4: 360. *t. 32.* 1925. TYPE: Brasil, Amazonas, Porto Velho, rio Madeira, 7 Sept. 1923, *Kuhlmann 17933* (RB, holotype; US, isotype); Albuquerque in Prance et al., Acta Amaz. 5:15. 1975.—Fig. 1A, Fig. 3.

Trees 10–30 m tall; branches 3–5-verticillate, quadrangulate; upper internodes densely buff-tomentellose, the lower internodes glabrescent. Leaves 3–5-verticillate, petiolate, the petioles 5–15(–20) mm long, densely buff tomentellose; leaf blades coriaceous, obovate, rounded to subemarginate at the apex, obtuse to acute at the base, 7–17 cm long, 3.5–11 cm wide, glabrous and prominently nerved above, tomentose below on the nerves, less densely pubescent on the surfaces, entire, slightly revolute, the lateral nerves 11–19 on each side, ascending, straight, anastomosing near the margins, subsulcate above, elevated below, the tertiary veinlets reticulately prominent on both sides. Inflorescence solitary in the upper axils, but several present among the crowded leaves; peduncles 3–6 cm long, densely buff-tomentose. *Staminate inflorescence:* Dichotomously 3-forked. Flowers sessile, few on each axis. Calyx deeply campanulate, 5–6 mm long, 3–4 mm wide, densely buff-appressed tomentellose without. Petals 15 mm long, the laminate portion linear-oblanceolate to ligulate-oblanceolate, 5 mm long, 1 mm wide, glabrous apically 3-lobed, the apical central portion 0.5–0.8 mm long, bordered by 2 lateral flanges 9–10 mm long, each lateral flange bearing 4–5 filamentous appendages basally attached to a lam-

inar portion 2 mm long; apical margin of the central portion bearing 3 short appendages 0.5–0.8 mm long on one side and 1 elongated appendage 9–10 mm long on other side. Stamens 10 in one equal series; filaments free in the upper 0.5 mm, united into a membrane at the base 1.5 mm long; anthers narrowly oblong, subemarginate, 1.2 mm long. Ovary rudiment conic, 1.7 mm long, 0.8 mm wide, densely buff tomentose or sericeous. *Pistillate inflorescence*: forked cyme with 2–3 flowers borne on each axis. Flowers subpedicellate; pedicels 0.5–1.5 mm long, densely buff-tomentellose. Calyx deeply campanulate, narrowed basally, 7–8 mm long, 4–5 mm wide above the base, 1.5 mm wide at the base; calyx lobes 5–7, triangular, acute, 1.5–2.7 mm long, 1.5–1.7 mm wide, sericeous within. Petals 5, 20–21 mm long, the laminar portion ligulate, 5 mm long, 1.5 mm wide, the fimbriate apical portion 15–16 mm long with 3 short middle appendages 1 mm long, and 2 lateral flanges bearing 4–5 elongate appendages, the united portion at the base 2.5–3 mm long, 0.7–1 mm wide. Ovary 5-celled, depressed-subglobose, subtruncate at the base, obtusely 5-angled, 2 mm long, 3 mm wide, densely tomentose. Staminodes 10, 0.8 mm long, the aborted anthers globose, 0.1 mm long and broad, the filamentous portion 0.6–0.7 mm long, united more than half-way down, the united portion 0.4 mm long at the base. Fruit obovate or oblong-obovate, 4 cm long, 2–2.5 cm wide, densely sericeous. Seed oblong, plano-convex, 8 mm long, 3.5–4 mm wide.

Specimens examined: BRAZIL. AMAZONAS: Municipality Humayta, near Livramento, rio Livramento, basin of rio Madeira, *Krukoff 6788* (NY), *7021* (NY, US); Manáos, circa Cachoeira do Mindú, *Ducke 23473* (US); Manáos, Colonia do Tarumá, *Ducke 23472* (NY, US); Borba, lower rio Madeira, *Ducke 23471* (US); Borba, rio Madeira, *Ducke 75* (NY, US); Manáos, *Ducke 10* (F); rio Urubú, igárapé Sangana, *Froes 25448* (NY); Manaus, a margem direita de Reserva Florestal Ducke, *Rodrigues, Coêlho & Coêlho 8468* (NY); Manáos, 25 m, *Killip & Smith 30197* (NY, US). PARA: Rio Tapajoz, circa cataractas Mangabal, 31 Aug. 1916 (fl.), 15 Dec. 1919 (fr.), *Ducke 6803*. TERR. RONDONIA: Brasilia-Acre highway, 66 km W of Vilhena, *Maguire, Pires, Maguire & Silva 56547* (NY). MATO GROSSO: Brasilia-Acre highway, 215 km W of rio Juruena, *Maguire, Pires, Maguire & Silva 56502* (NY); 20 km E of Vilhena, 670 m, *Maguire, Pires, Maguire & Silva 56805* (NY, VEN). PERU. LORETO: Mishuyacu, near Iquitos, 100 m, Feb.–Mar. 1930, *Klug 897* (NY, US).

2. **Sterigmapetalum guianense** Steyermark, Fieldiana Bot. 28(2): 422. 1952. TYPE: Venezuela, Estado Bolívar, dense forest at base of cerro along río Karuai, Ptari-tepui, 1,220 m, 27 Nov. 1944, *Steyermark 60658* (F, holotype).—Fig. 1B, C.

Trees 15–20 m tall; branches 3–4-verticillate, terete; upper internodes sericeous, the lower internodes glabrous. Stipules ovate-triangular, obtuse, 6–8 mm long, 2–2.5 mm wide, densely sericeous both sides. Leaves 3–4-verticillate, shortly petiolate, the petioles 5–9 mm long, glabrous to densely sericeous, leaf blades coriaceous, broadly cuneately obovate to obovate- or oval-oblong, subtruncate to slightly emarginate or rounded at the apex, subobtuse to acute at the base, 3.5–8 cm long, 2–7 cm wide, the margins remotely and inconspicuously minutely glandular-denticulate to entire, mainly glabrous except the midnerve beneath sparsely to more densely appressed-pubescent, the lateral nerves 9–12 on each side, arcuate-ascending, anastomosing before the margins, prominently impressed above in subsp. *guianense*, elevated below, the tertiary veinlets conspicuously impressed above in subsp. *guianense*, absent or obsolete in subsp. *ichunense*, conspicuously reticulate below. Inflorescence 1 to 3, terminal or in the axils of the uppermost leaves, compactly dichotomously cymose. *Staminate inflorescence*: peduncles 0.3–3 cm long with two main axes 1.5–2 mm long, moderately to densely appressed-pubescent or pilosulous, 12–15-flowered. Flowers white, on short pedicels 1.5–2 mm long or subsessile, 6–8 mm long, 5 mm wide, 5-merous. Bracteoles narrowly lanceolate, subobtuse, 1.5–2 mm long, 0.5 mm wide, pilosulous both sides, involucrate. Calyx 5-dentate, urceolate, 4–5.5 mm long, 3–3.5 mm wide, glabrous to sparsely pilosulous without, densely sericeous within, the teeth triangular-ovate, subacute, 1.5 mm long. Petals 5, spatulate, dorsally densely pilose, ventrally sparsely pilose, subunguiculate toward the base, 6 mm long at maturity, 1.8 mm wide apically, the central cucullate portion shorter than the lateral flanges, provided with an incurved penicillate tuft; lateral flanges exceeding the central portion, 1.5–2.5 mm long, 3–4-fimbrillate, the appendages glabrous. Stamens 10; filaments unequal, 3–4 mm long, united in the basal 1 mm, glabrous; anthers broadly oblong, 1 mm long. Staminodes squamelliform, 1 mm long, bordering the basal sides of the filaments, united with the base of the filaments. Ovary rudiment densely hirsute. *Pistillate inflorescence*: Fruit obovate, 16 mm long, 8 mm broad, densely appressed-pubescent.

KEY TO THE SUBSPECIES OF *STERIGMAPETALUM GUIANENSE*

1a. Upper leaf surface with prominent and subreticulate tertiary venation .... 2a. *S. guianense* subsp. *guianense*
1b. Upper leaf surface lacking pronounced or subreticulate tertiary venation .... 2b. *S. guianense* subsp. *ichunense*

2a. Sterigmapetalum guianense Steyerm. subsp. **guianense**

Geographical distribution: Talus slopes and dwarf forest on sandstone table mountains at 1,585–1,615 m altitude in southeastern Estado Bolívar, Venezuela, and dwarf forest bordering savanna at 550–565 m altitude at base of Tafelberg Mountain, Surinam (Fig. 3).

Specimens examined: VENEZUELA. BOLIVAR: Ptari-tepui, *Steyermark 60658* (pistillate plant, type of *S. guianense* subsp. *guianense*, F, holotype); Ptari-tepui, SE slopes bordering quebradas at base of slopes, *Steyermark 60042* (F, US, VEN); vicinity of "Misia Kathy Camp", on mesa between Ptari-tepui and Sororopán-tepui, 1,615 m, *Steyermark 60288* (F). SURINAM: South Savanna No. I, Tafelberg, 565 m, *Maguire 24737* (F, NY); 200 m, south Savanna No. IV, Tafelberg, 550 m, *Maguire 24780* (NY).

2b. Sterigmapetalum guianense subsp. **ichunense** Steyermark & Liesner, subsp. nov. TYPE: Venezuela, Bolívar, Sierra Ichún, laderas boscosas y filas al sur del Salto María Espuma (Salto Ichún), a lo largo del río Ichún, tributario del río Paragua, 4°46'N, 63°18'W, 500–625 m, 29 Dec. 1961, *Julian A. Steyermark 90428* (VEN, holotype; NY, US, isotype).—Fig. 2: 1.

A subsp. *guianense* differt nervulis tertiariis foliorum supra haut manifestis vel obsoletis.

Geographical distribution. Sandstone forested areas in southern Venezuela at 110–500 m (Fig. 3).

Additional specimens examined: VENEZUELA. BOLIVAR: Sierra Ichún, *Steyermark 90428* (US, VEN). TERR. FED. AMAZONAS: San Carlos de Río Negro, dense forest alrededores del aeropuerto, 125 m, 17–18 Aug. 1970, *Steyermark & Bunting 102747* (US, VEN); road from San Fernando de Atabapo to Santa Bárbara, 12–40 km from San Fernando, 110 m, 24 Mar. 1974, *Gentry & Tillett 10868* (MO, VEN).

The specimens cited from Terr. Fed. Amazonas tend to have longer petioles and shorter pubescence. Additional collections with flowers from that region may eventually show that an additional subspecies or species is represented.

3. Sterigmapetalum exappendiculatum Steyermark & Liesner, sp. nov. TYPE: Venezuela, Bolívar, montane forest, cumbre of La Escalera, Alto río Cuyuni, río Uiri-Yuk, 1,000 m, Aug. 20–21 1962, *Maguire, Steyermark & Maguire 46876* (VEN, holotype; NY, isotype).—Fig. 2: 2.

Arbor 12–20-metralis, ramulis juvenilibus internodiis superioribusque dense pallido-tomentellis; stipulis ovato-lanceolatis subobtusis 7–10 mm longis, 3.5–5 mm latis dense sericeis; foliis 3-verticillatis, petiolis 5–11 mm longis sericeis; laminis subcoriaceis oblongis vel elliptico-oblongis apice rotundatis vel late obtusis raro acutis, basi obtusis vel subacutis 7–14 cm longis 3.7–8 cm latis supra praeter costam sparsim pilosam glabris, subtus modice vel dense adpreso-pilosis costa dense sericea, marginibus utroque latere 11–15 crenulato-denticulatis, nervis lateralibus utroque latere 10–12 adscendentibus ante marginem 4–10 mm anastomosantibus supra conspicue impressis subtus elevatis, venulis tertiariis utrinque manifeste reticulatis elevatisque; inflorescentiis solitariis pedunculatis in axillis foliorum supremorum insidentibus, pedunculis 2–3 cm longis dense breviter puberulis; inflorescentiis foemineis juvenilibus congestis multifloris, bracteis 3–5 mm longis 1–1.5 mm latis; calyce 5-dentato utrinque sericeo; petalis juvenilibus obovato-subdolabriformibus dorsum superneque papillatis ventraliter inferneque pilosulis, apice breviter pilosulis, parte media apicali incurvata tribus appendicibus brevibus instructa, petalorum appendicibus lateralibus nullis; ovario juvenili ovoideo apice obtuse dense hirsutulo 5-lobato basi squamellis circumcincto.

Trees 12–20 m tall; young branches and upper internodes densely tomentellous. Stipules ovate-lanceolate, subobtuse, 7–10 mm long, 3.5–5 mm wide, densely sericeous. Leaves 3-verticillate, the petioles 5–11 mm long, sericeous; leaf blades subcoriaceous, oblong or elliptic-oblong, rounded or broadly obtuse, rarely acute, at the apex, obtuse or subacute at the base, 7–14 cm long, 3.7–8 cm wide, glabrous above except sparsely pilose on the midnerve, moderately or densely appressed-pilose below, the midrib densely sericeous, each margin with 11–15 crenulate denticulations, the lateral nerves ascending, 10–12 on each side, anastomosing 4–10 mm from the margin, conspicuously impressed above, elevated below, the tertiary veins manifestly reticulate and elevated both sides. Inflorescence solitary, pedunculate, from the uppermost leaf axils; peduncles 2–3 cm long, densely short puberulous. *Young pistillate inflorescence*: congested, many-flowered, the bracts 3–5 mm long, 1–1.5 mm wide. Calyx 5-dentate, sericeous within and without. Young petals obovate-subdolabriform dorsally and above papillate, ventrally and below

pilosulous, the apex shortly pilosulous, the median portion incurved at the apex bearing 3 short appendages, the appendages none. Young ovary ovoid, obtuse at the apex, densely hirsutulous, 5-lobed, surrounded at the base by squamellae.

PARATYPES: VENEZUELA. BOLIVAR: Chimantá Massif, vicinity of Bluff Camp, at base of west-facing sandstone bluffs of Chimantá-tepui (Torono-tepui), 1,700 m, 2–4 June 1954, *Steyermark 75634* (NY, VEN); vicinity of km 143, south of El Dorado, NE of Luepa, 1,200 m, 6–11 Mar. 1962, *Steyermark & Aristeguieta 47* (US, VEN).

Geographic distribution: Montane forests overlying the Roraima sandstone formation, southeastern Estado Bolívar, Venezuela, at 1,000–1,700 meters (Fig. 3).

This species is well-marked by the absence of lateral appendages of the petals, sparse indument of the petals, crenulate-denticulate leaves, and rather densely tomentose stems, peduncles, and lower surface of leaf blades.

4. **Sterigmapetalum colombianum** Monachino, Trop. Woods 77: 10. 1944. TYPE: Colombia. Magdalena: Río Jabalí region (La Victoria), 1,000–1,200 m, Dec. 1931–Feb. 1932, *Espina & Giacometto A31* (NY, holotype; F, isotype).

Tree 10–25 m tall; uppermost internodes apparently glabrous but covered by a minute, densely appressed indument. Stipules ovate, subacute, 1.5–2 mm long, 1.2 mm wide, appearing somewhat resinous in bud. Leaves 3–4-verticillate, shortly petiolate, the petioles 2–6 mm long, apparently glabrous but basally with minute hairs; leaf blades subcoriaceous, obovate, rounded at the apex, cuneately acute at the base, 4.5–6.7 cm long, 2–4 cm wide, glabrous on both sides (minute scattered, pale, appressed hairs may be present beneath), entire, the lateral nerves 8–12 on each side, ascending, anastomosing 3–5 mm from the margin; tertiary veins finely reticulate and elevated on both surfaces. *Pistillate inflorescence:* solitary, shortly pedunculate in the axils of the uppermost leaves; peduncles 8–10 mm long, 1–3-flowered, densely minutely appressed-pubescent. Flowers umbellate, sessile (in bud only). Calyx (in bud) apparently 5-dentate, sparsely appressed-pubescent or practically glabrous without, densely appressed-pubescent within. Petals (immature) subobovate, glabrous except ventrally slightly sericeous in the lower half, two lateral flanges each bearing 4–6 glabrous fimbrillae, the apex of the middle portion between the lateral flanges bearing a tuft of short hairs. Staminodia 10, scalelike and united at the base into an annulus (according to Monachino). Ovary spheroid, pubescent, 5-angulate.

Geographical distribution: Forests of northeastern Colombia, in Department of Magdalena, at 1,000–1,200 m (Fig. 3).

Two collections, in addition to the type, from the Department of Magdalena, Colombia, both sterile, were identified by Standley as *S. colombianum* and cited by Monachino (1944). The data for these collections are: Cincinnati region, 1,300–1,500 m, Dec. 1931–Feb. 1932, *Espina & Giacometto A142,* and Río Toribio region, slope of San Lorenzo, 1,000–1,200 m, *Espina & Giacometto A90.*

The description of this species is incomplete and unsatisfactory, due to the 1) immature development and fragmentary nature of the inflorescence, and 2) uncertainty of presence or absence of indument on the type collections. Monachino described the species from the NY holotype as having peduncles only "ca. 3 mm long," but an examination of the F isotype shows peduncles 8–10 mm long. The peduncles and uppermost part of the stems in the NY holotype appear to be covered by a microscopically dense appressed indument, but the F isotype is covered by minute hyphal threads that complicate the interpretation of the presence or absence of indument. Similarly, the calyx tube on the F isotype is covered by fungal hyphae to the extent that uncertainty remains as to whether the exterior surface is completely glabrous or bears some minute appressed indument.

Monachino described the NY holotype as having an inflorescence composed only of the bud of female flowers, "single on end of peduncle" (1944), but the F isotype shows three peduncles arising just below the apical portion of the twigs, each peduncle bearing 3 sessile flowers. In the publication of the Amazonian species of Rhizophoraceae (Albuquerque in Prance et al., 1975), the pedicels of *S. colombianum* are stated to be 3 mm long, whereas this length refers actually to the peduncles of the NY holotype as described by Monachino, since the flower buds themselves are strictly sessile.

The two specimens cited by Albuquerque under *S. colombianum* for Venezuela and Surinam respectively (*Steyermark 90428* and *Maguire 24780*) are treated in the present paper as *S.*

guianense subsp. *ichunense* and *S. guianense* subsp. *guianense.* Additionally, a specimen collected by *de la Cruz 2170* from Guyana (NY) and identified as *S. colombianum,* proves to belong to the Malpighiaceae.

5. Sterigmapetalum tachirense Steyermark & Liesner, sp. nov. TYPE: Venezuela. Tachira: cloud forested ridge top, along steep slopes leading to Cerro Azul, at Cerro Las Minas, 18 km southeast of Santa Ana, 7°36'N, 72°13'W, 1,200–1,380 m, 11 Nov. 1979, tree 20 m tall, leaves coriaceous, spreading, rich green above, pale green below, petals white, calyx pale green, *Julian A. Steyermark, Ronald Liesner & Angel González 120032* (VEN, holotype; MO, isotype).—Fig. 4.

Arbor 20-metralis, ramulis juvenilibus dense minuteque papillato-pubescentibus indumento adpreso munitis; stipulis non visis; foliis 3-verticillatis raro oppositis brevipetiolatis, petiolis 2–2.5 mm longis minute papillato-puberulentibus vel glabrescentibus; laminis suborbiculari-ovalibus apice rotundatis basi rotundatis 6–8.5 cm longis 5.3–7 cm latis utrinque glabris integerrimis; nervis lateralibus utroque latere 12–13 divaricate patentibus ante marginem 2–7 mm anastomosantibus; inflorescentiis masculinis solitariis in axillis foliorum supremorum pedunculatis; pedunculis 1.2–1.7 cm longis sparsim vel modice minuteque adpresso-puberulentibus pilis papillatis instructis, cymoso-ramosis, axibus secundariis 4–5 mm longis minute adpreso-puberulentibus flores crebros gerentibus; floribus masculinis breviter pedicellatis, pedicellis 0.5 mm longis; calyce profunde campanulato 3.5–4 mm longo 2–2.8 mm lato, tubo 2.5 mm longo extus sparsim adpreso-puberulenti glabrescenti intus sparsim adpreso-piloso; calycis lobis 4 deltoideo-ovatis obtusis 1.2–1.5 mm longis 1.3 mm latis extus praeter apicem ciliolatum glabris intus dense adpresso-pubescentibus; petalis 4 anguste oblanceolato-ligulatis 5 mm longis basi 0.5 mm latis, superne 1.5 mm latis basim versus unguiculatis, ungue 1.5 mm lato; petalis apice 3-lobatis, parte centrali cucullata segmentis aggregatis incurvatis munita, utroque latere extensionibus duobus lateralibus in 15–18 fimbrias elongatas glabras fissis, infra segmentos laterales marginesque dense hispidulis; staminibus 8, filamentis 3.5 mm longis 0.2 mm latis basi 0.5 mm longis connatis; antheris anguste oblongis 1.2–1.5 mm longis 0.4 mm latis; staminodiis subulatis apice paullo angustatis 1 mm longis; ovarii rudimento conico 1 mm longo basi 0.7 mm lato adpresso-piloso.

Trees 20 m tall; juvenile branches covered with dense, minute, appressed papillate indumentum. Stipules not seen. Leaves 3-verticillate, rarely opposite, short-petioled, the petioles 2–2.5 mm long, minutely papillate-puberulent or glabrescent; leaf blades suborbicular-oval, rounded at the apex, rounded at the base, 6–8.5 cm long, 5.3–7 cm wide, entire, both sides glabrous, the lateral nerves 12–13 each side, divaricately spreading, anastomosing 2–7 mm from margin. *Staminate inflorescence*: solitary in axils of the uppermost leaves; cymosely branched, the secondary axes 4–5 mm long, minutely appressed-puberulent; peduncles 1.2–1.7 cm long, sparsely or moderately appressed-puberulent, the hairs papillate; flowers in close succession. Flowers with pedicels 0.5 mm long. Calyx deeply campanulate, 3.5–4 mm long, 2–2.8 mm wide, the tube 2.5 mm long, sparsely appressed-puberulent, glabrescent without, sparsely appressed-pilose within. Calyx lobes 4, deltoid-ovate, obtuse, 1.2–1.5 mm long, 1.3 mm wide, glabrous without except for the ciliate apex, within densely appressed-pubescent. Petals 4, narrowly oblanceolate-ligulate, 5 mm long, 0.5 mm wide at the base, upwards 1.5 mm wide, unguiculate toward the base, the claw 1.5 mm wide; petal apices 3-lobed, the central part cucullate, provided with incurved, clustered segments, on each side with two lateral flanges parted into 15–18 elongate, glabrous fimbria, the lateral segments below and the margins densely hispid-pubescent. Stamens 8; filaments 3.5 mm long, 0.2 mm wide at the base, connate in the basal 0.5 mm; anthers narrowly oblong, 1.2–1.5 mm long, 0.4 mm wide; staminodes subulate, somewhat narrowed at the apex, 1 mm long. Ovary rudiment conical, 1 mm long, 0.7 mm wide at the base, appressed-pilose.

Geographical distribution: Montane forests of Estado Táchira, western Venezuela, at 1,200–1,380 m elevation (Fig. 3).

This species differs from the other known members of the genus in its tetramerous flowers with 4 calyx lobes, 4 petals, and 8 stamens, and in the suborbicular-oval leaves rounded at both ends.

Sterigmapetalum subgenus **Balsamocaulon** Steyermark & Liesner, subgenus novum. TYPE: *Sterigmapetalum resinosum* Steyermark & Liesner.

Exsudatum resinosum adest. Folia opposita. Extensiones laterales petalorum deminutae vel obsoletae.

6. Sterigmapetalum resinosum Steyermark & Liesner, sp. nov. TYPE: Venezuela. Bolívar: selva humeda en las laderas del Cerro Uei, entre los brazos del río Uei (afluente del río Venamo y Cuyuni), km 121.5 south of El Dorado, 1,050 m, 27–28 Dec. 1970, tree 2[illegible] m, leaves coriaceous, deep green above, dull

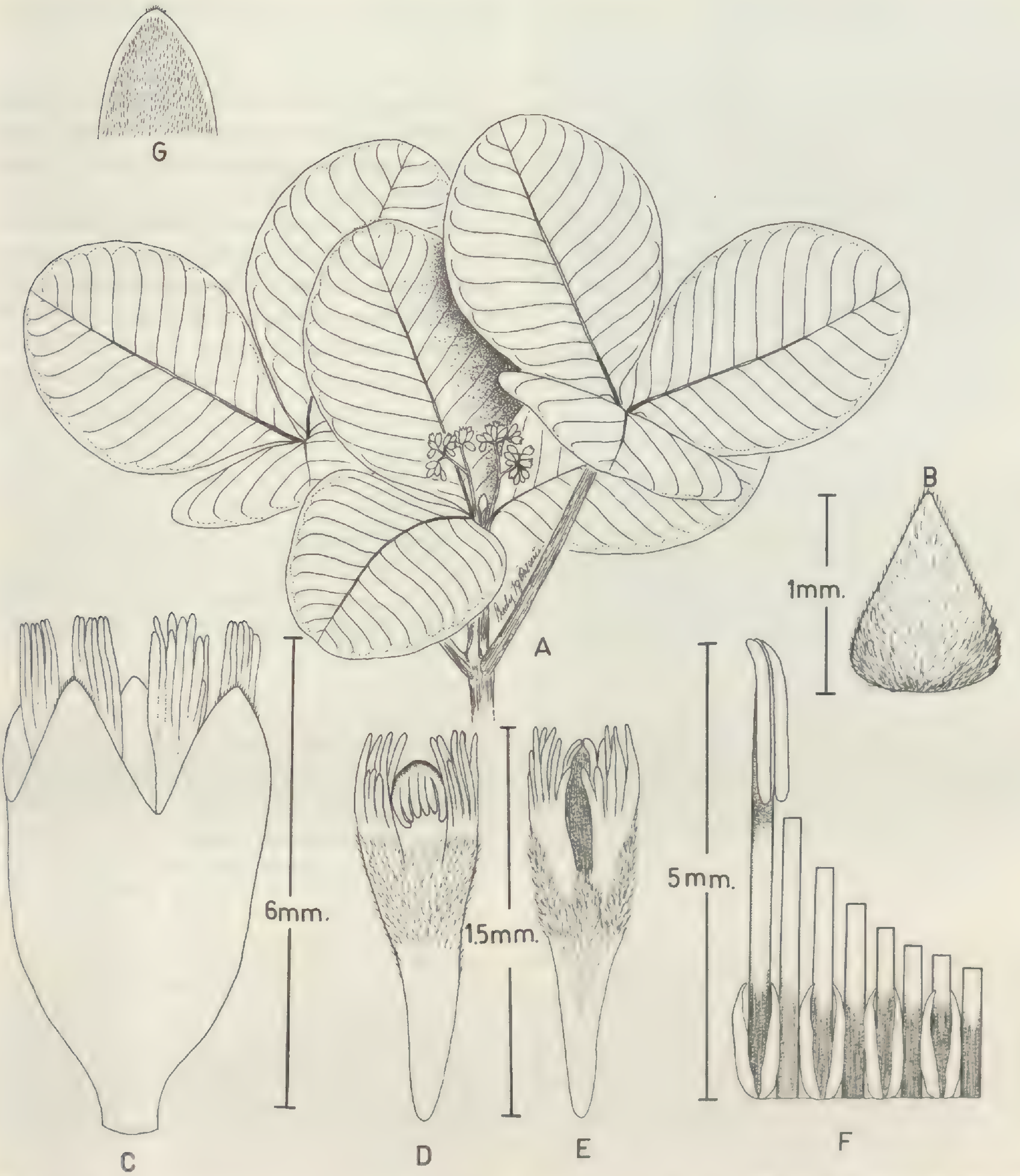

FIGURE 4. *Sterigmapetalum tachirense.* A. Habit, flowering branch, ×1. B. Ovary rudiment, staminate flower. C. Staminate flower, lateral view. D. Petal, ventral view, staminate flower. E. Petal, dorsal view, staminate flower. F. Androecium, staminate flower, showing one complete stamen, the other stamens with portions of filaments attached to basal membrane. G. Inner upper surface of calyx lobe.

green below, *Julian A. Steyermark, G.C.K. & E. Dunsterville 104569* (US, holotype, sheet No. 2581558-A; US, isotype, sheet 2581559-A).—Fig. 2: 3.

Arbor 20–25-metralis, ramulis glabris vel glabrescentibus, internodiis supremis resinosis; stipulis supremis subresinosis lanceolato-ovatis acutis vel acuminatis 4–5 mm longis glabris demum caducis; foliis oppositis petiolatis, petiolis 10–15 mm longis glabris vel glabrescentibus, laminis coriaceis oblongo-ellipticis vel oblanceolato-oblongis apice abrupte angustatis acutis vel obtuse acutis basi acutis 5–10.5 cm longis 2–5 cm latis utrinque glabris subtus obsolete minuteque glanduloso-punctatis, marginibus utroque latere 15–16-subcrenulatis in sinubus glanduliferis; nervis lateralibus utroque latere 11–14 ad angulum 20–25° patentibus supra impressis subtus paullo elevatis ante marginem 2–4 mm anastomosantibus, venulis tertiariis subtus aliquantum manifestis subreticulatisque supra vix manifestis; inflorescentiis masculinis (imma-

turis) resinosis solitariis in axillis nodorum supremorum secundorum usque ad sextos breviter pedunculatis insidentibus, pedunculis (immaturis) 1–1.7 cm longis minute parceque puberulis ca. 6-floris; floribus breviter pedicellatis in cymis ramosis dispositis, pedicellis in alabastro 0.5 mm longis; calyce in alabastro 2 mm longo subcoriaceo 5-angulato, lobis 5 deltoideo-ovatis subacutis marginibus elevatis apice pilosis extus aliter glabris intus superne minute pilosulis aliter glabris; petalis 5 (immaturis) panduriformibus apice rotundatis cucullatis, appendices tres subulatas incurvatas gerentibus basi rotundatis 0.8 mm longis 0.3 mm latis utrinque glabris dorsum obtuse carinatis, extensionibus lateralibus nullis; staminibus 10 (immaturis), filamentis brevissimis basi dilatatis connatis; ovarii rudimento ovoideo-conico apice rotundato glabro 5-angulato; stigmate sessili.

Trees 20–25 m tall; branches glabrous or glabrescent; uppermost internodes resinous. Uppermost stipules subresinous, lanceolate-ovate, acute or acuminate, glabrous, 4–5 mm long, caducous. Leaves opposite, petiolate, the petioles 10–15 mm long, glabrous or glabrescent; leaf blades coriaceous, oblong-elliptic or oblanceolate-oblong, the apex abruptly narrowly acute or obtusely acute, the base acute, 5–10.5 cm long, 2–5 cm wide, both surfaces glabrous, abaxially obsoletely minutely glandular punctate, each margin with 15–16 subcrenulate teeth, the sinuses glandular, the lateral nerves on both sides 11–14, spreading at a 20–25° angle, adaxially impressed, abaxially slightly elevated, anastomosing 2–4 mm from the margin, the tertiary veins abaxially more or less manifestly subreticulate, adaxially scarcely manifest. *Male inflorescence*: (immature) resinous, solitary, in axils of the second to the sixth uppermost nodes shortly pedunculate; peduncles (immature) 1–1.7 cm long, minutely sparsely puberulous ca. 6-flowered; flowers short-pedicellate in branched cymes, the pedicels in bud 0.5 mm long. Calyces in bud 2 mm long, subcoriaceous, 5-angled, 5-lobed, the lobes deltoid-ovate, subacute, margins elevated, abaxially pilose at the apex, otherwise glabrous, minutely pilose within, otherwise glabrous. Petals 5, (immature), panduriform, rounded, cucullate at the apex, the appendages three, subulate, incurved, the base rounded, 0.8 mm long, 0.3 mm wide, both sides glabrous, dorsally obtusely keeled, the lateral appendages absent. Stamens 10 (immature); filaments very short, dilated and connate at the base. Ovary rudiment ovoid-conical, the apex rounded, glabrous, 5-angled; stigma sessile.

PARATYPE: VENEZUELA. BOLÍVAR: En el drenaje del río Cuyuni, a lo largo del río Anawaray-parú, vecindades del km 134 y campamento 134 al sur de El Dorado, 1,300–1,350 m, 25 Dec. 1970, *J. Steyermark, G.C.K. & E. Dunsterville 104463* (US, VEN).

Geographic distribution: Montane forests over Roraima sandstone formation of Estado Bolívar, southeastern Venezuela, at 1,050–1,300 m elevations.

This species is distinguished by the resiniferous exudate on the apical portion of the stem, buds, and peduncles, the opposite leaves with abruptly acute apex, and glabrous petals which lack lateral flanges.

7. **Sterigmapetalum heterodoxum** Steyermark & Liesner, sp. nov. TYPE: Venezuela. Falcón: Sierra de San Luis, Montaña de Paraguariba, forested area bordering savanna, entre el Hotel Parador y Curimagua, 1,300 m, 21 July 1967, tree 3 m, leaves coriaceous, deep green above, paler green below, flower buds green with 5 valvate sepals, *Julian A. Steyermark 99409* (VEN, holotype; US, isotype).—Fig. 2: 4.

Arbor 3-metralis, ramulis glabris, internodiis superioribus resinosis; stipulis suborbiculari-ovatis obtusis glabris resiniferis; foliis oppositis petiolatis, petiolis 8–11 mm longis glabris, laminis coriaceis obovatis apice truncato-rotundatis basi cuneatis 5.5–9 cm longis 3.5–5 cm latis utrinque glabris, marginibus inconspicue 11–12-crenulatis in sinubus minute glanduliferis, nervis lateralibus utroque latere 10–11 ad angulum 15–20° divaricate patentibus ante marginem 2–5 mm anastomosantibus, supra subimpressis inconspicuis subtus subelevatis, venulis tertiariis subtus minute reticulatis supra obsoletis; inflorescentiis masculinis (immaturis) resinosis solitariis in axillis nodorum supremorum secundorum usque ad sextos breviter pedunculatis insidentibus, pedunculis (immaturis) 1.2–1.5 cm longis glabris ca. 5-floris; floribus (immaturis) ut videtur subsessilibus resinosis; calyce in alabastro 3.5 mm longo extus glabro intus sericeo 5-dentato, dentibus apice pilosulis marginibus elevatis induratis; petalis 5 (immaturis) dorso superne pilosis, marginibus ciliatis aliter glabris, apice parte centrali cucullata hispida, appendices tres subulatas incurvatas gerentibus, utroque latere extensionibus duobus lateralibus inaequalibus erectis appendices duas subulatas gerentibus; staminibus 10 inaequalibus in alabastro, filamentis brevissimis 0.6 mm longis basi connatis; ovarii rudimento columnari-subconico 0.6 mm longo.

Trees 3 m tall; branches glabrous; upper internodes resinous. Stipules suborbicular-ovate, obtuse, glabrous, resinous. Leaves opposite, the petioles 8–11 mm long, glabrous; leaf blades coriaceous, obovate, the apex truncate-rounded, the base cuneate, 5.5–9 cm long, 3.5–5 cm wide, both sides glabrous, the margins inconspicuously 11-

12 crenulate-toothed, the sinuses minutely glandular, the lateral nerves on both sides 10–11, divaricately spreading at a 15–20° angle, anastomosing 2–5 mm from the margin, above inconspicuously subimpressed, below subelevated, the tertiary veins below minutely reticulate, above obsolete. *Male inflorescence*: (immature) resinous, solitary, in the axils of the second to sixth uppermost nodes; peduncles (immature) 1.2–1.5 cm long, glabrous, about 5-flowered. Flowers (immature) apparently subsessile, resinous. Calyces in bud 3.5 mm long, glabrous without, sericeous within, 5-dentate, the teeth pilose at the apex, the margins elevated, indurated. Petals 5 (immature); dorsally pilose above, the margins ciliate, otherwise glabrous; central part of the apex cucullate, hispid, bearing 3 subulate, incurved appendages, each side bearing 2 lateral, unequal, erect, subulate appendages. Stamens 10, unequal in bud; filaments short, 0.6 mm long, basally connate. Ovary rudiment conical-subconical, 0.6 mm long.

This species, like the foregoing *S. resinosum*, is well-marked by the resiniferous exudate on the upper internodes, buds, and peduncles, characteristic of subgenus *Balsamocaulon*, and by the opposite leaves. It differs from *S. resinosum* in having the leaves truncate-rounded at the apex, stipules obtuse, and petals densely pilose at the apex with lateral flanges bearing two unequal fimbrillate appendages.

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NEW SPECIES AND COMBINATIONS IN THE GENUS *OENOTHERA* (ONAGRACEAE)[1]

WARREN L. WAGNER[2]

ABSTRACT

Four new combinations in *Oenothera* sect. *Megapterium* and one each in sects. *Pachylophus* and *Oenothera* are made here to make them available for use in regional floras. *Oenothera harringtonii* (sect. *Pachylophus*) from southeastern Colorado, *O. clelandii* (sect. *Oenothera* subsect. *Raimannia*) principally from the Great Lakes region south to Iowa and Illinois, and *O. heterophylla* subsp. *orientalis* from two disjunct areas in Alabama and Arkansas are newly described here in order to also make them available.

A series of revisionary papers on *Oenothera* sects. *Megapterium* (Wagner, in prep.), *Pachylophus* (Wagner et al., in press), and *Oenothera* subsects. *Oenothera* (Dietrich & Wagner, in prep.) and *Raimannia* (Dietrich et al., in prep.) that contain new taxa and combinations are currently in press or in the late stages of preparation. The publication of one or more regional floras that contain information resulting from these detailed studies on *Oenothera*, however, will likely precede that of the revisions. Therefore, in order to make these new names and combinations available for the *Great Plains Flora*, the *Vascular Flora of the Southeastern United States*, vol. 3, and the *Michigan Flora*, vol. 2, they are published here in advance of the revisions. Detailed discussion of these changes and new taxa will be included in the revisions.

Oenothera sect. *Megapterium* (Spach) Endl.

Oenothera macrocarpa Nutt. subsp. **incana** (A. Gray) W. L. Wagner, comb. et stat. nov.

Oenothera missouriensis Sims var. *incana* A. Gray, Boston J. Nat. Hist. 6: 189. 1850. TYPE: "Canadian River" probably in the Texas Panhandle in one of the following counties—Oldham, Potter, Hutchinson, Roberts or Hempshill—Texas, April 1848, *A. Gordon 31* (GH, lectotype, photo MO; MO, isolectotype; Munz, Amer. J. Bot. 17: 366. 1930).

Oenothera macrocarpa Nutt. subsp. **oklahomensis** (Nort.) W. L. Wagner, comb. et stat. nov.

Megapterium oklahomense Nort., Annual Rep. Missouri Bot. Gard. 9: 153. 1898. TYPE: Marena, Payne County, Oklahoma, 1893, *F. A. Waugh 183* (MO-2529631, lectotype here designated; KSC, US, isolectotypes). Munz (Amer. J. Bot. 17: 365. 1930) selected the US specimen as the lectotype, however, Norton apparently only examined the KSC and MO sheets.

Oenothera macrocarpa Nutt. subsp. **fremontii** (S. Wats.) W. L. Wagner, comb. et stat. nov.

Oenothera fremontii S. Wats., Proc. Amer. Acad. Arts 8: 587. 1873. TYPE: "White rock on Smoky Hill River," Ellsworth, Russell, Ellis, Trego, Cove, or Logan county, Kansas, 7–23 June 1867, *C. C. Parry 79* (GH, lectotype here designated; MO 3 sheets, US, isolectotypes). Munz (Amer. J. Bot. 17: 367. 1930) indirectly selected the Fremont collection (second expedition), also mentioned by Watson, as the lectotype. Since GH has no Fremont collection that could be the one Watson saw I have selected the other collection cited by Watson, *Parry 79*, as the lectotype.

Oenothera macrocarpa is a variable species that has differentiated extensively in the Great Plains region. Each of the four subspecies occupies a different geographical and ecological situation and in general they are sharply distinct. They are treated as subspecies primarily because of their complete interfertility and extensive intergradation in any area of marginal contact. Intermediates are known between *O. macrocarpa* subsp. *macrocarpa* and subspp. *fremontii* and *oklahomensis* and between subspp. *oklahomensis* and *incana*. There is also evidence that suggests past hybridization between subspp. *incana* and *fremontii*, although there is at present no contact between them.

[1] This material is based upon research supported by a grant to Peter H. Raven from the National Science Foundation.

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Oenothera howardii (A. Nels.) W. L. Wagner, comb. nov.

Lavauxia howardii A. Nels., Bot. Gaz. (Crawfordsville) 34: 368. 1902, non M. E. Jones, Zoe 3: 301. 1893. TYPE: "In clay, Vermilion," Sevier Co., Utah, 1,600 m, 16 July 1894, *M. E. Jones 5631c* (RM-13996, lectotype here designated; BM, G, MO 2 sheets, MSC, NY, POM, UC, US, isolectotypes). Jones's publication of the name *Oenothera howardii* is invalid since he proposed the name in anticipation of its future acceptance (Art. 34.lb, International Code of Botanical Nomenclature, 1978). He placed his discussion of "*Oenothera howardii*" under the name *Oenothera johnsonii* Parry (= *O. primiveris* A. Gray) and stated that should the entity prove distinct he named it *O. howardii.* Thus the first valid publication of the epithet was by Aven Nelson as *Lavauxia howardii.* I am grateful to Dan Nicolson for his helpful comments on this situation.

Oenothera brachycarpa sensu Munz, Amer. J. Bot. 17: 367. 1930, pro parte.

Plants from Hamilton Co., Kansas, eastern Colorado, Utah, and Nevada formerly included in *Oenothera brachycarpa* are segregated here as *O. howardii.* This species is quite distinct from *O. brachycarpa* in its brilliant yellow petals that dry reddish brown, floral tubes 4.3–11(–12.5) cm long and in that it consists of entirely tetraploid, hexaploid, and octoploid plants whereas *O. brachycarpa* from west Texas to southeastern Arizona and northern Mexico has pale yellow petals that dry lavender, floral tubes (10.5–)12–22 cm long and is entirely diploid, $n = 7$.

Oenothera L. sect. *Pachylophus* (Spach) Endl.

Oenothera caespitosa Nutt. subsp. **macroglottis** (Rydb.) W. L. Wagner, Stockhouse & Klein, comb. et stat. nov.[3]

Pachylophus macroglottis Rydb., Bull. Torrey Bot. Club 30: 259. 1903. TYPE: "Turkey Creek and tributaries," in present vicinity of La Veta Pass, Heurfano Co., Colorado, 2,800–2,900 m, 8 & 9 June 1900, *P. A. Rydberg and F. K. Vreeland 5857* (NY, holotype, photo MO; RM, isotype). Locality reconstructed with the aid of R. Barneby (pers. comm.).

The plants treated here as *Oenothera caespitosa* subsp. *macroglottis* were included by Munz (1931, 1965) within his broadly defined and artificial *O. caespitosa* var. *montana* (Nutt.) Durand. Slightly curved capsules (1.7–)2.5–5.6 cm long with an undulate ridge along the valves, coarsely dentate spatulate to broadly oblanceolate leaves and cool montane habitat clearly distinguish this entity from the other subspecies of *O. caespitosa.* It ranges from southern Wyoming, Colorado to southeastern Utah and northern New Mexico.

Oenothera harringtonii W. L. Wagner, Stockhouse & Klein, sp. nov. TYPE: United States: Colorado, El Paso Co., Colorado Springs, 2,000 m, 29 May 1939, *J. H. Ehlers 7461* (MICH, holotype, photos MO, COLO; MICH 2 sheets, NA, isotypes).

Oenothera caespitosa var. *eximia* sensu Munz, Amer. J. Bot. 18: 731. 1931, pro parte (as to plants from Colorado).

Herba annua caulescens. Folia tenuia, hirtella pilis minutis glandulosis. Tubus floralis 3.1–6 cm longus. Petala alba demum pallido-subrosea, 2–2.6 cm longa. Capsula lanceoloidea, recta, (2.1–)2.5–3(–3.5) cm longa, valvularum marginibus 6–8 tuberculis prominentibus 2–3 mm altis interdur coalescentibus porcam sinuatam formantibusque, per dimidium velduos longitudinis trientes deshiscens. Numerus chromosomaticus gameticus, $n = 7$.

This attractive species named in honor of the late Harold D. Harrington (1903–1981) is known only from grasslands in the southeastern Colorado counties of El Paso, Fremont, Otero, and Las Animas. *Oenothera harringtonii* is distinctive in the *O. caespitosa* complex in being a coarse annual with densely leafy, erect stems; capsules ovoid with 5–8 conspicuous tubercles 2–3 mm high and five or more flowers opening at one time.

Oenothera L. sect. *Oenothera* subsect. *Oenothera*

Oenothera elata H.B.K. subsp. **hirsutissima** (A. Gray ex S. Wats.) Dietrich, comb. et stat. nov.[4]

Oenothera biennis L. var. *hirsutissima* A. Gray, Mem. Amer. Acad. Arts II. 4: 43. 1849; ex S. Wats., Proc. Amer. Acad. Arts 8: 579. 1873. TYPE: Valley of Santa Fe Creek, Santa Fe Co., New Mexico, June 1847, *A. Fendler 218* (GH, lectotype; MIN, MO, isolectotypes; Munz, Aliso 2: 18. 1949).

Recent careful study of a large number of spec-

[3] This combination and *O. harringtonii* are contributed jointly with R. Stockhouse, Pacific University, Forest Grove, OR 97166 and W. M. Klein, Morris Arboretum, 9414 Meadowbrook, Philadelphia, PA 19188.

[4] Contributed by W. Dietrich, Botanisches Institut of the University of Düsseldorf, Germany.

imens of plants assigned to *Oenothera hookeri* Torr. & A. Gray and *O. elata* suggested that the two entities are extremely similar and should be recognized as one species (Raven et al., 1979; Dietrich & Wagner, unpubl.) Populations in the United States and northern Mexico can be separated from those from coastal California and those from central Mexico south to Panama and are here recognized as *O. elata* subsp. *hirsutissima.*

Oenothera L. sect. *Oenothera* subsect. *Raimannia* (Rose) Dietrich

Oenothera clelandii Dietrich, Raven & W. L. Wagner, sp. nov.[5] TYPE: United States: Michigan. Mason Co., Amber Township, E half of sec. 23 NE ¼, 30 September 1974, *C. J. Barkley s.n.* (MO-2383779, holotype; MO, isotype).

Oenothera rhombipetala sensu Munz, N. Amer. Fl. II. 5: 108. 1965, pro parte.

Herba biennis. Inflorescentia compacta, non interrupta ramis lateralibus; efflorescent flores complures per diem. Petala late elliptica vel ovata, acuta (raro rotundata), 0.5–1.6 cm longa, flava vel pallide flava. Antherae spargunt pollen ipse in stigmate per anthesin. Semina ambito elliptica, brunnea, 1–1.9 mm longa. Numerus chromosomaticus gameticus, $n = 7$; planta chromosomatice structuraliter heterozygotica.

This distinctive new species is a complex structural heterozygote. A ring of 14 chromosomes is thus formed at meiotic metaphase I and the pollen is only about 50% fertile. Populations formerly included in *Oenothera rhombipetala* from southeastern Minnesota and Michigan south to Iowa, Illinois and scattered localities in Arkansas, Missouri, Kentucky, New Jersey, and New York are all autogamous complex heterozygotes and are here separated from the larger-flowered, outcrossing, fully fertile, pair-forming populations from South Dakota south to Texas and central Arkansas. *Oenothera clelandii* is named in honor of Ralph E. Cleland (1892–1970), lifelong student of *Oenothera* cytogenetics.

Oenothera heterophylla Spach subsp. **orientalis** Dietrich, Raven & W. L. Wagner, subsp. nov. TYPE: United States: Alabama, Sumter Co., sandy clay field, 5.2 mi S of Dancy, 3 May 1972, *R. Kral 46366* (MO-2379457, holotype; DUKE, GA, GH, NCU, NY, USF, VDB, isotypes).

Tubus floralis 3–4.7 cm longus, immaculatus, sine pilis pustulatis. Sepala immaculata, sine pilis pustulatis, apices sepalorum 1–3 mm longi, erecti. Ovarium et capsula saepe omninoglabrum. Numerus chromosomaticus gameticus, $n = 7$.

Oenothera heterophylla subsp. *orientalis* is clearly distinguished from subsp. *heterophylla*, which occurs from central and eastern Texas to eastern Louisiana, in its lack of red pustulate hairs on any flower parts, sepal-tips erect in bud, 1–3 mm long and the ovary glabrous. It is known from only two disjunct areas: Greene, Pickens and Sumter counties in Alabama and Calhoun, Nevada, and Ouachita counties in Arkansas.

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[5] This species and the next subspecies contributed in collaboration with W. Dietrich and Peter H. Raven, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166.

NOTES

CONFIRMATION OF THE CHROMOSOME NUMBER IN CEPHALOTACEAE AND RORIDULACEAE

Cephalotaceae (monotypic) and Roridulaceae (ditypic) are two Southern Hemisphere families of restricted distribution. *Cephalotus* is endemic to southwestern Western Australia and *Roridula* to the Cape region of South Africa. The two families share little in common apart from their being insectivorous in that they derive supplementary nitrogen from insects and other small organisms trapped by their leaves. *Cephalotus* is herbaceous and has relatively large leaves that produce pitchers, while the two species of *Roridula* are shrubby and have small leaves covered with sticky but evidently not glandular hairs.

Because of the intrinsic interest of these families as well as the taxonomic difficulties surrounding them, and because living material was available, we embarked on a cytological study and have determined the chromosome number in *Cephalotus* and one species of *Roridula*. Initially we believed that both families were unknown cytologically (Raven, 1975) but the work of Kondo (1969), Keighery (1979), and Johnson (1980), in which the base number of x = 10 was established for *Cephalotus* has now come to our attention. In addition, Kress (1970), published chromosome numbers for both *Cephalotus* and *Roridula*. Kress found $2n = 12$ in *Roridula gorgonias* and also recorded $2n = 20$ in *Cephalotus*. These numbers are here confirmed, meiotic material having been studied in the case of *Cephalotus*. Since no illustration of the chromosomes of *Roridula* has previously been published, a photograph (Fig. 1) of a metaphase spread is included here. Chromosome number and voucher information are as follows:

Cephalotus follicularis Labill. $n = 10$. Western Australia, Flinders Park, Albany, *Ornduff 8823* (UC).

Roridula gorgonias Planch. $n = 6$. South Africa, Cape, Vogelgat, Hermanus, *Williams 2790* (MO).

We thank Ion Williams, Vogelklip, Hermanus, South Africa for the seed of *Roridula*; and R.

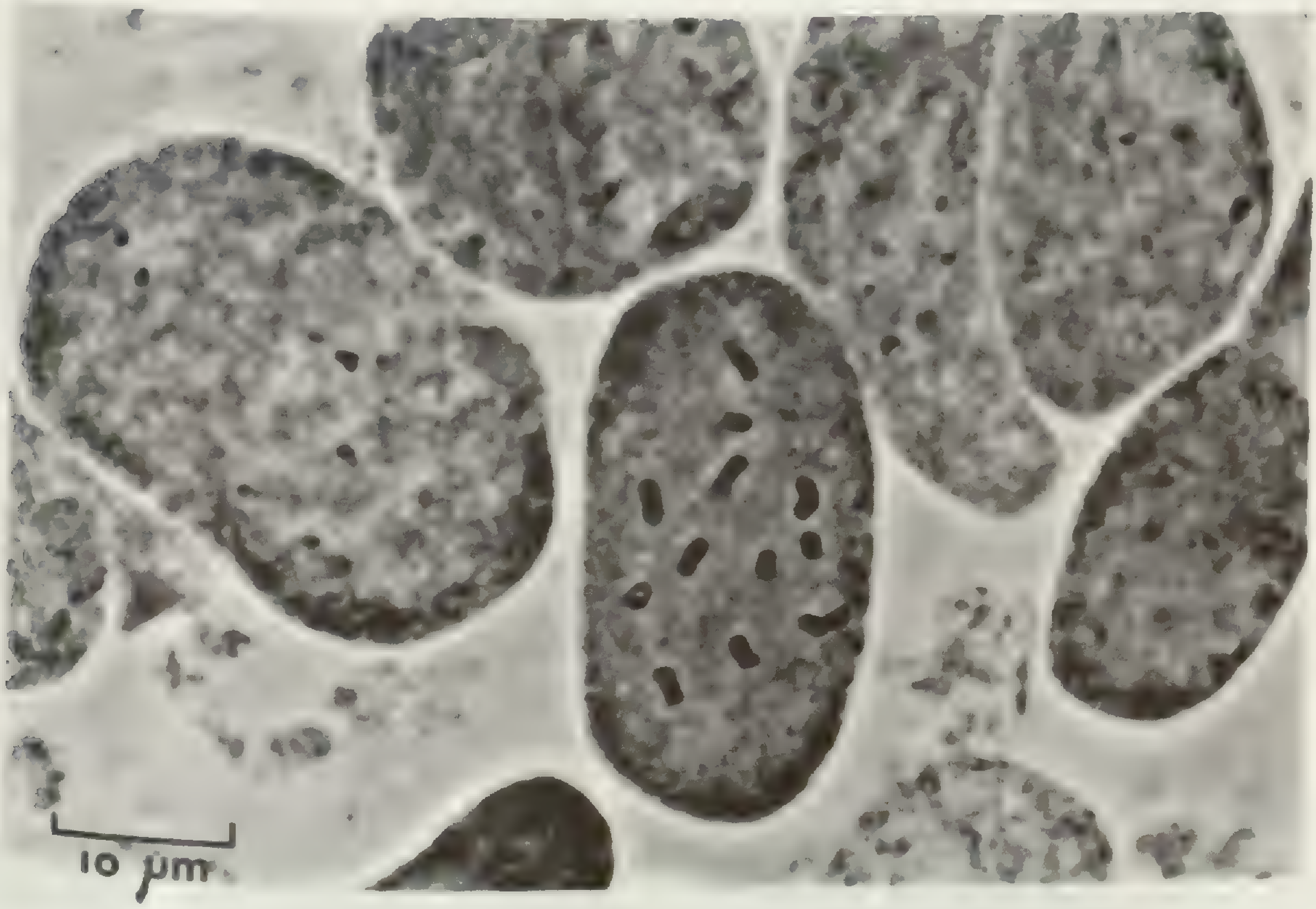

FIGURE 1. Mitotic metaphase in *Roridula gorgonias*.

Ornduff, University of California, Berkeley for providing the fixed buds of *Cephalotus*.

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A NEW *HESPEROMANNIA* (COMPOSITAE) FROM MAUI ISLAND: HAWAIIAN PLANT STUDIES 116

Hesperomannia (Compositae) consists of three species and four subspecific entities, mostly endemic to the single islands, Kauai, Oahu, Molokai, and Maui. They are attractive trees, with flower heads like large pink thistles. Now, another species has been discovered in west Maui.

Hesperomannia mauiensis sp. nov. HOLOTYPUS: Hawaiian Islands, west Maui Island, Iao Valley, Makalaloa Stream, steep forested slope, July 22, 1980, *Robert Hobdy 859* (BISH).—Fig. 1.

Diagnosis Holotypi: Arbor 2.3–3.3 m alta est, petiolis 17–30 mm longis in basi puberulis, laminis 9.5–16 cm longis 4–7.5 cm latis chartaceis ellipticis acutis varie subacuminatis cuneatis subintegribus glabris, inflorescentia terminali ascendente puberula cum 4–5 capitibus, involucro 30–32 mm alto dense ascendente puberulo, phyllariis superis lineari-lanceolatis, flosculis 30–40 luteis, corollis cum tubo 15–17 mm longo lobis 12 mm longis 0.3 mm latis extra pilosulis, antheris 7–8 mm longis, aculeis pappi 27 mm longis.

Tree 2.3–3.3 m tall; leafy branchlets 2.5–5 mm in diameter, terete, brown, densely pale ascending puberulous; leaves in a plume at the branchlet tips; internodes 2–8 mm long; nodes scarcely enlarged; leaf scars 6–7 mm wide, lunate; bundle scars 7; petioles 17–30 mm long, puberulous only at base; blades 9.5–16 cm long, 4–7.5 cm wide, stiff chartaceous, elliptic, acute to subacuminate, the base cuneate, the margins subentire but undulate, above dark green, glabrous, below green, glabrous, secondary veins 7–9 in each half, ascending, the lower ones straight, the upper arcuate; inflorescence terminal, racemose, with 4–5 heads, densely ascending puberulous; peduncle 2–5 mm long, 2.5–3 mm in diameter; pedicels 7–12 mm long; involucre 30–32 mm high, narrowly campanulate, with numerous imbricated phyllaries, these pinkish, but densely pale ascending puberulous, the lowest ones 2–3 mm long, ovate, acute, the median ones lanceolate, 3.5 mm wide, the upper ones linear lanceolate; florets 30–40, canary yellow; ovary 5.5 mm long, prismatic, puberulous; corolla tube 15–17 mm long, glabrous, the 5 lobes 12 mm long, 0.3 mm wide, almost linear, but tapering to an acute tip, sparsely pilosulous without, with a midrib; filaments 7–8 mm long; anthers 7–8 mm long, almost linear, finally splitting apart; style exserted, dark; pappus bristles 38, and 27 mm long, stramineous, mostly upwardly barbellate (mature achenes not seen).

The closest relative of this novelty is *H. arborescens* Gray ssp. *Swezeyi* (Deg.) Carlq., a plant with the blades oblanceolate (or narrowly so) or obovate, obtuse or subobtuse; all or at least the inner phyllaries glabrous; corolla tube 20 mm long, the lobes 18 mm long, 1.5 mm wide; anthers 9 mm long; and the pappus bristles 50. *Hesperomannia mauiensis* has the blades elliptic, acute to subacuminate; phyllaries all ap-

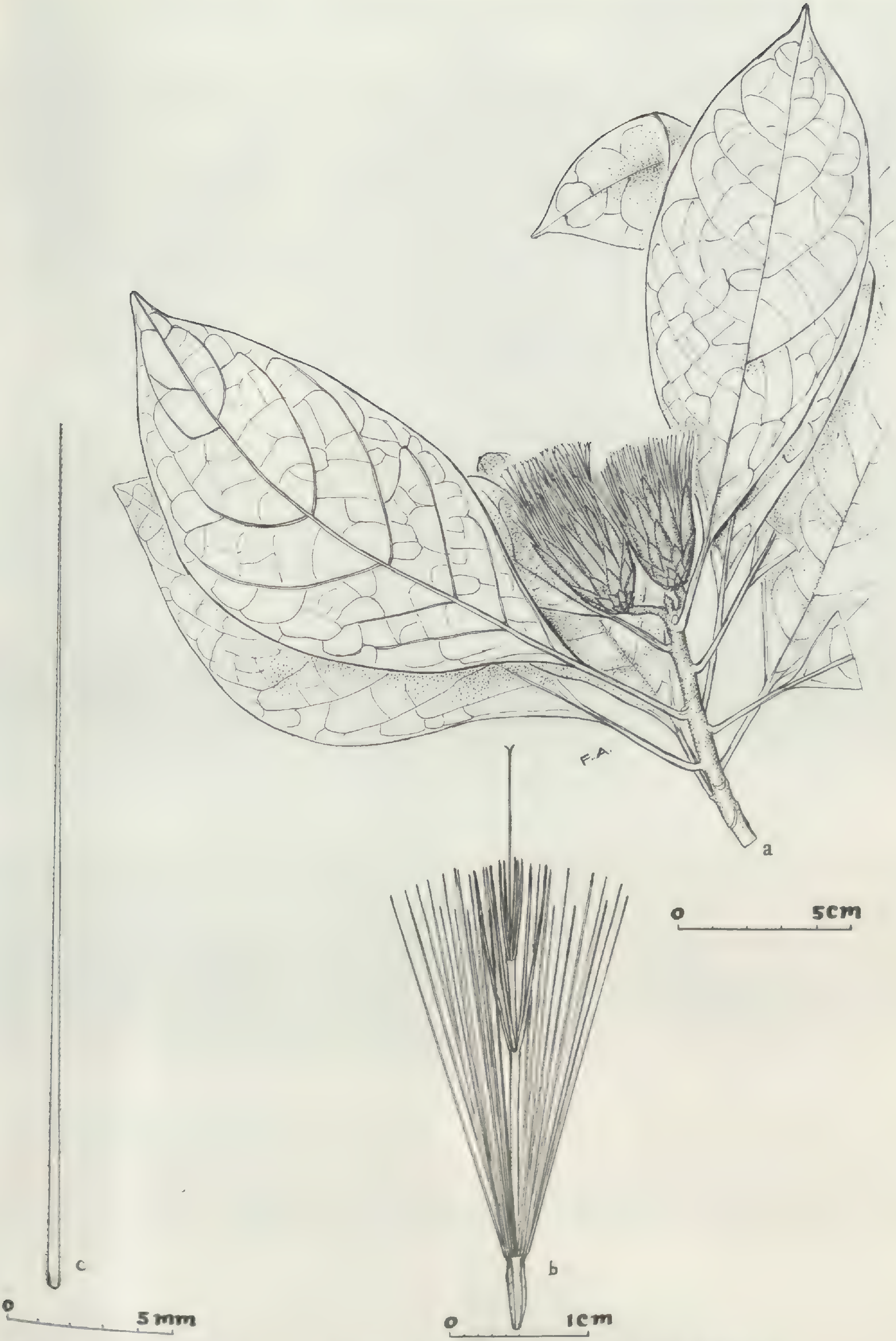

FIGURE 1. *Hesperomannia mauiensis* St. John, from holotype. *a*, habit, ×½; *b*, floret, ×2.

pressed puberulous; corolla tube 16–17 mm long, the lobes 12 mm long, 0.3 mm wide; anthers 8 mm long; and the pappus bristles 38.

The new epithet is formed from the name of the type locality, Maui, and *-ensis*, the Latin adjectival place ending.

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TORTULA CHISOSA SP. NOV., A BISTRATOSE-LEAVED SPECIES FROM THE UNITED STATES, MEXICO, AND SOUTHERN AFRICA

Tortula chisosa Magill, Delgadillo et Stark, sp. nov. is described here from material collected in North America and southern Africa. It is closely related to *T. ammonsiana* and *T. bartramii.*

In 1976, one of us reported the occurrence of an unusual specimen of *Tortula* from the mountains of west Texas (Magill, 1976). The specimen (*Magill 1341*) was of interest because of a unique combination of characters that separated it from all North American species of *Tortula.* In connection with a study of mosses of Zacatecas, Mexico (Delgadillo & Cárdenas, 1979), four specimens that are nearly identical with the Texas plants were obtained; L. Stark and R. C. Castetter collected five others in New Mexico, and R. Magill secured two additional collections in southern Africa. Comparison of these specimens against specimens and descriptions of other taxa suggests that the first represent an undescribed species of *Tortula.*

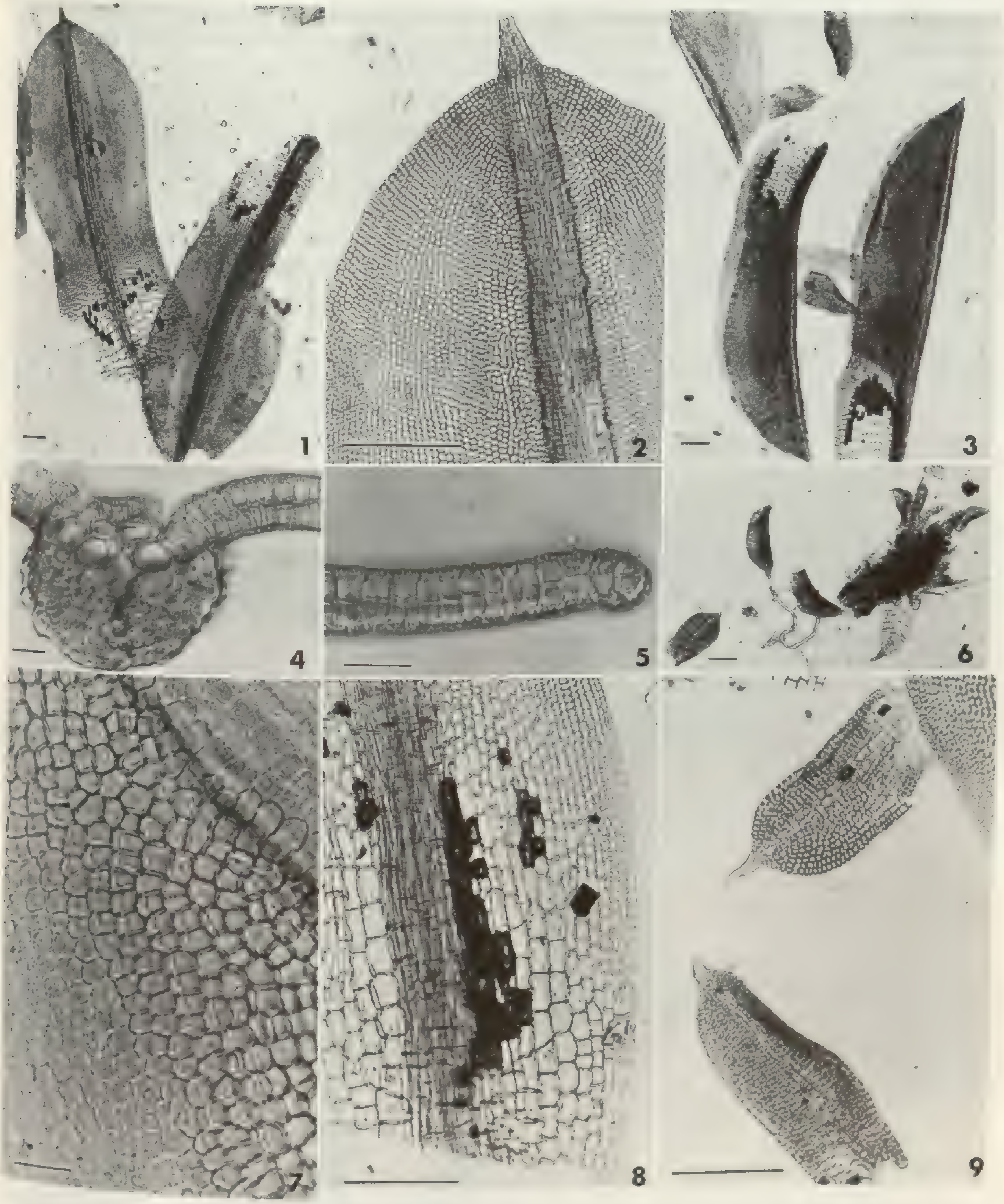
Tortula chisosa Magill, Delgadillo et Stark, sp. nov.

Habitu et forma foliorum et propagulorum *T. ammonsiana* Crum et Anderson simile, sed foliis bistratosis et apicibus sine denticulatis et costa dorsali supra papillosa differt.

Plants with the habit of *T. ammonsiana.* Stem up to 6 mm tall, loosely tufted, dark brown to nearly black when dry, with a small central strand and an inconspicuous hyalodermis. Leaves loosely appressed when dry, erect spreading when moist, 0.5–0.7(–0.8) mm wide, 1.2–2.3 mm long, smaller toward the base of the stem, crowded near the tip, oblong to spatulate. Leaf blade bistratose, entire; margins plane; upper and median leaf cells quadrate or hexagonal, firm-walled, 8–13 μm in diameter, with several hollow c-shaped papillae per lumen; basal leaf cells hyaline, quadrate to rectangular, smaller toward margin, forming distinct fenestrations on lower third or fourth of the leaf. Costa reddish, excurrent as a short mucro, dorsally papillose on the upper third to halfway down, 58–103(–113) μm wide at midleaf, in section with a strong dorsal stereid band of 4–7 layers of cells, 2–4 guide cells and 2–4 adaxial papillose cells; the hydroid group is inconspicuous. Propagulae in groups on stalks in axils of upper leaves, stalked, costate, leaflike, with upper cells papillose, ending in a single hyaline smooth-walled apical cell, that may be subtended by 2 or 3 smooth-walled cells. Perichaetial leaves not differentiated. Male inflorescence and sporophyte unknown.

TYPE: U.S.A. TEXAS: Big Bend National Park, Chisos Mountains, on soil in small canyon below Lost Mine Trail, W side Lost Mine Peak, ca. 1,600 m, 19 June 1973, *Magill 1341* (MO, holotype).

Additional specimens examined: U.S.A. NEW MEXICO: Doña Ana Co., ca. .25 mi E of Dripping Springs area, W side Organ Mountains, 32°19′N, 106°34′W, 2,072 m, 10 July 1980, *Stark & Castetter 1154* (MEXU, PAC). Filmore Canyon, Organ Mountains, 32°21′N, 106°35′W, 1,813 m, July 1981, *Stark & Castetter 3102A, 3105A, 3106A, 3107A* (PAC). MEXICO. ZACATECAS: Cerro de la Bufa, 22°47′N, 102°34′W, 2,700 m, Junio 1979, *Cárdenas 332b* (MEXU); 2 km E Gualterio, Mpio. Chalchihuites, 23°35′N, 103°49′W, 2,250 m, Marzo 1981, *Cárdenas 1077c* (MEXU); La Boquilla, 7 km S Sombrerete, 23°34′N, 103°38′W, 2,380 m, Marzo 1981, *Cárdenas 1113* (MEXU); 8 km N Pinos, 22°22′N, 101°35′W, 2,590 m, Marzo 1981, *Cárdenas 1195* (MEXU). LESOTHO: 233 km E of Maseru, S of St. Theresa, canyon along Orange River, Dec. 1977, *Magill 4242* (MEXU, PRE). SOUTH WEST AFRICA: Buchuberg summit, S Namib, Sept. 1977, *Williamson 2675d* (MEXU, PRE).



FIGURES 1–9. *Tortula chisosa.*—1. Leaves.—2. Leaf apex.—3. Leaves and propagulae.—4. Median cross-section of costa showing dorsal papillae.—5. Median cross-section of leaf margin.—6. Propagulae and stalk.—7. Upper laminal cells, costa at upper right corner.—8. Basal leaf cells and right basal leaf margin.—9. Propagulae showing costal development. (All *Magill 1341*). Bars equal 0.1 mm in Figures 1, 2, 3, 6, 8, 9 and 20 μm in Figures 4, 5, and 7.

This new species is distinguished from other species of *Tortula* by the plane, mucronate-spatulate leaves with reddish, papillose costae, bistratose laminae; the production of stalked, clustered, costate, leaf-like propagulae; and a terricolous or saxicolous habitat. This combination of character states is remarkably constant but not exempt from variation in the collections

thus far analyzed. For example, the leaf laminae, while consistently bistratose in all specimens, in several cases show unistratose patches in mid-leaf cross sections. Stalked propagulae have not been observed in three specimens: *Cárdenas 1077c, Magill 4242,* and *Williamson 2675d,* even though other diagnostic features are present. The last specimen has additional variations that are of interest in the evaluation of the species; its leaf cells are consistently smaller (7–10 μm) than those of the American collections and the angle of leaf blade insertion is steeper. Also, the leaves are keeled, a fact that is not evident on other specimens.

Tortula chisosa is similar in many respects to *T. caninervis* (Mitt.) Broth. (syn. *T. bistratosa* Flowers); however, in the latter species the plants are larger, the leaf margins are recurved, and the leaves awned. Through the production of leaf-like propagulae, *T. chisosa* is also related to the *T. pagorum-laevipila* complex. The similarities in habit and habitat, leaf form and method of propagule production clearly indicate relationship to *T. ammonsiana.* This last species was described from the eastern United States (Crum & Anderson, 1979) and would appear to be one of the closest relatives of *T. chisosa.* However, the differences between them are clear; the leaves of *T. chisosa* are bistratose, they lack minute apical teeth (also absent in African specimens of *T. ammonsiana*), and the costa is papillose dorsally toward the apex.

In New Mexico *Tortula chisosa* has been found intermixed with plants of *T. bartramii* Steere; study of both plants from the same sites has shown that they are similar in cell size, stem, and costal structure. Leaves of *T. bartramii* had occasional bistratose patches and, in one instance, one plant showed a few small apical leaves that resembled the propagulae of *T. chisosa.* Despite this, the combination of character states by which we define our new species is maintained and allows easy separation of mixed samples. The nature of factors promoting appearance of leaf-like propagulae and bistratosity are beyond the scope of this paper, but, undoubtedly, they should be explored before a final evaluation of the relationships of *T. chisosa* and *T. bartramii.*

The present known distribution of *T. chisosa* may at first appear unusual. However, it apparently parallels that of several better-known species, e.g., *Aloina bifrons, Anacolia laevisphaera, Tortula pagorum,* and *Trichostomopsis australasiae.* Thus, we would expect to find *T. chisosa* in South America or Australia to complement its occurrence in Africa.

We would like to acknowledge the valuable comments of Mr. Brent Mishler, and the field assistance of Mr. R. C. Castetter; Miss A. Cárdenas kindly provided her collections for analysis. Contribution No. 220 from the Department of Biology, The Pennsylvania State University.

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POLYGALA DUKEI (POLYGALACEAE), A NEW SPECIES FROM PANAMA

Polygala dukei K. Barringer, sp. nov. TYPE: Panama. Darien: the Bolimina, small hill, *Duke & Brista 385* (US!).—Fig. 1.

Ab *P. scleroxylon* Ducke ramulis inermis foliis alternis bracteis glabris setas paucis subtentis differt.

Small tree with hard wood, white bark. Stems glabrous, without spines, with persistent leaf bases at the nodes. Leaves alternate, glabrous; petioles to 6 mm long, rugulose, drying darker than the blade; blade ovate-lanceolate, entire, subcoriaceous, shiny, 9–13 cm long, 4–7 cm wide, the base cuneate, the apex acuminate, the margin slightly revolute when dry, the midvein impressed above, prominent below, the secondary veins prominent on both surfaces, irregularly reticulate. Inflorescences axillary, racemose; axis 5 mm long; bracts glabrous, rigid, 1 mm long, subtended by a few stiff bristles. Flowers unknown. Calyx deciduous. Capsule green, glabrous, loculicidal, 2-loculate, 1.5 cm long, 2.2 cm wide, conspicuously 2-lobed, the lobes ovoid, not winged; locules 1-seeded; seed smooth, glabrous, globose, pendulous, with an umbraculiform aril.

Additional Collection: PANAMA. DARIEN: near Estero Grande off Río Marea, 13 May 1967, *Duke 10965* (MO!).

Duke reports that the fruits are tasteless and odorless and are eaten by currasow, parrots, and parakeets.

The type is without flowers, but the fruits, habit, and leaf venation place it in *Polygala* section *Acanthocladus.* Chodat (1891, 1896) defined the section by its usually thorny stems, flowers in axillary fascicles, and stiff bracts. He keyed the section on the basis of its deciduous calyx, keeled petals, undivided stigma, and glabrous, un-

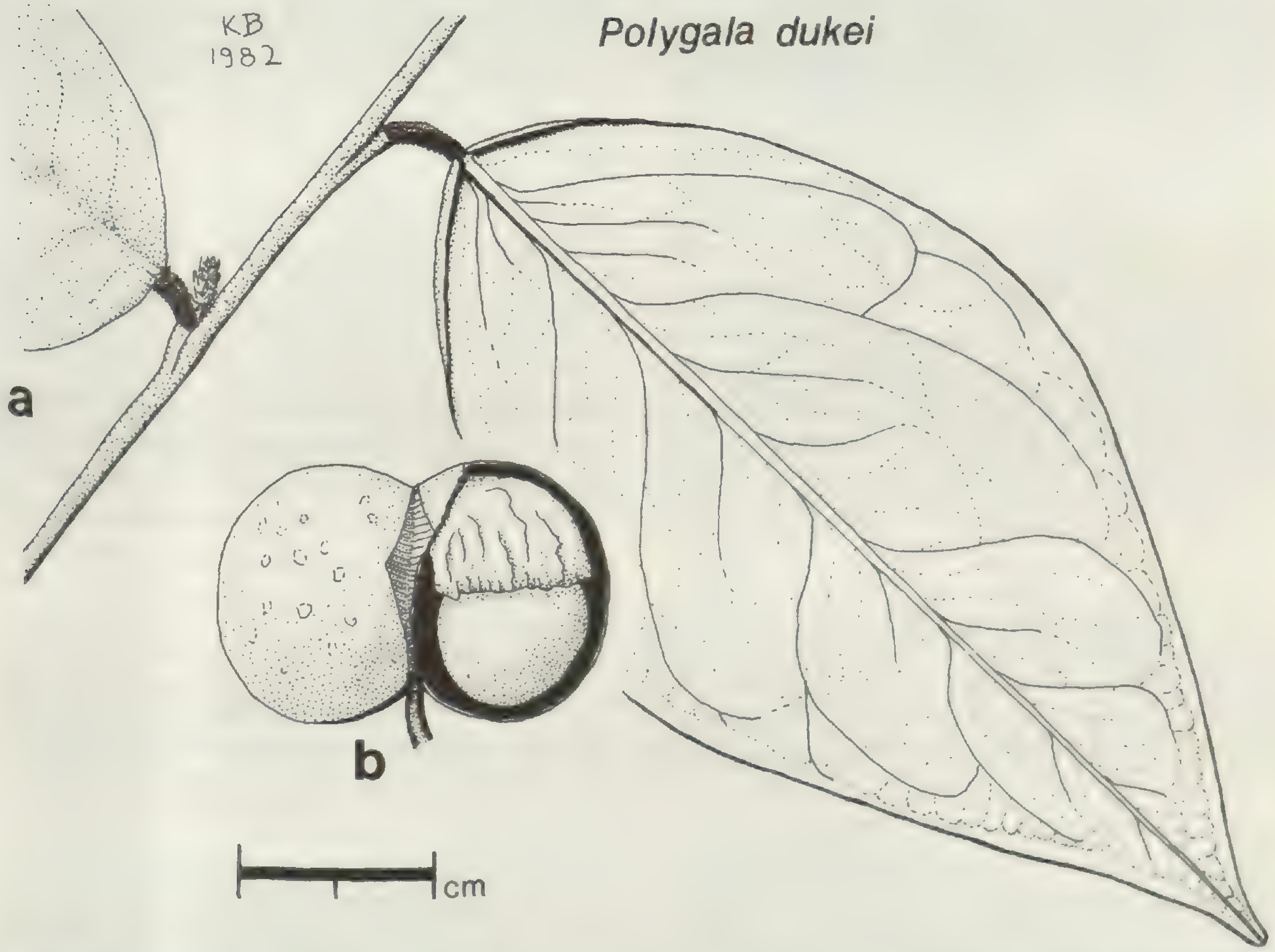

FIGURE 1. *Polygala dukei* K. Barringer. a. portion of branch with remnants of axillary inflorescence. b. fruit with part of valve removed to show aril and seed. Upper portion of scale indicates fruit size, lower portion indicates habit size, units equal 1 cm.

winged fruit. He described two species, *P. klotzschii* Chod. and *P. bennettii* Chod. [= *P. albicans* (Bennett) Grondona], both from Brazil. Later, two more Brazilian species were described, *P. pulcherrima* Kuhlm. and *P. scleroxylon* Ducke. All four species are trees or shrubs with opposite leaves and persistent leaf bases. Short lateral branches often become spines after the leaves fall. The inflorescences are very short racemes, so that the flowers are fasciculate in leaf axils. The calyx is deciduous and the fruit is conspicuously 2-lobed, each lobe being ovoid and containing a single, pendulous, arillate seed. The leaves are subcoriaceous and have prominent looped secondary veins and irregularly reticulate tertiary veins. *Polygala dukei* shares all these characters except presence of spines and opposite leaves.

Polygala dukei can be easily distinguished from all other Panamanian species by its arborescent habit, its fasciculate, axillary flowers, and its 2-lobed fruits (Lewis & Herrera-MacBryde 1969).

I would like to thank Robin Foster for pointing out the problem. William Burger, Michael Nee, and Michael Huft helped by critiquing the manuscript. Research was supported in part by NSF Grant DEB 8103184 to the Field Museum.

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A NEW VARIETY OF *DECLIEUXIA CACUMINIS* (RUBIACEAE) FROM BAHIA

Among Raymond M. Harley's Rubiaceae from Bahia, Brazil, are numerous collections of *Declieuxia* H.B.K., of which there are two gatherings of *D. cacuminis*. This species has been previously reported from Minas Gerais (Kirkbride, 1976).

One of these collections, *Harley et al. 21216* from the Serra Geral de Caitité, is referrable to *D. cacuminis* var. *decurrens* Kirkb. which was known only from the type collection and two paratype collections, all from the vicinity of Grão Mogol (Kirkbride, 1976), approximately 350 air-kilometers south-southwest of the new station. In my discussion of the pubescence of var. *decurrens* (Kirkbride, 1976), it was described as less densely puberulous and with longer hairs on the mericarps than var. *cacuminis*. The pubescence of *Harley et al. 21216* is denser with shorter hairs on the mericarps than the type collections. So the variation of pubescence in var. *decurrens* encompasses that found in var. *cacuminis*.

The other collection represents a new variety, which is presented here:

Declieuxia cacuminis Müller Argoviensis var. **glabra** Kirkbride, var. nov.

Frutex omnino glaber, stipulis trilobis, decurrentibus, corollis caeruleis, fructibus apicis incisura 0–0.4 mm, mericarpiis 2.2–2.4 × 2–2.2 mm, ca. 0.6 mm crassis.

TYPUS: Brazil, Bahia, Serra das Almas, middle and upper N.E. slopes of Pico das Almas, ca. 25 km W.N.W. of the Vila do Rio de Contas, ca. 41°57′W, 13°33′S, alt. 1,600–1,850 m, *Harley et al. 19691* (holotypus, UB; isotypus, CEPEC, K).

The overall appearance of this variety is ericoid, and therefore similar to that of var. *cacuminis*. It is easily separated from the other two varieties by its totally glabrous condition and other details that are set forth in the following key to the varieties of *D. cacuminis*:

1a. Shrubs completely glabrous; mericarps with the emargination 0–0.4 mm deep .... *D. cacuminis* var. *glabra*

1b. Shrubs or subshrubs puberulous except the calyx and sometimes the corolla glabrous; mericarps with the emargination 0.5–1 mm deep.

  2a. Stipules unidentate or tridentate, not decurrent; corolla blue, externally sparsely puberulous; mericarps 2.2–2.6 × 1.6–1.8 mm, 0.7–0.9 mm thick .... *D. cacuminis* var. *cacuminis*

  2b. Stipules unidentate, decurrent; corolla white, externally glabrous; mericarps 1.5–

2.1 × 0.8–1.1 mm, 0.2–0.4 mm thick .... *D. cacuminis* var. *decurrens*

The varieties of *D. cacuminis* are an example of taxa whose distribution at the highest elevations in the Serra do Espinhaço and further north in Bahia is correlated with their differentiation. These may have resulted from either long distance dispersal and random selection of genotypes or Pleistocene climatic changes with drastic alterations in the distribution of the vegetation and resulting differentiation (Kirkbride, 1976). In my opinion, the latter is more important in this case and in the genus *Declieuxia.*

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A NEW COMBINATION FOR A PROBLEMATIC CENTRAL AMERICAN APOCYNACEAE

Prestonia woodsoniana (Monachino) A. Gentry, comb. nov. *Echites woodsoniana* Monachino, Bull. Torrey Bot. Club 86: 245. 1959. TYPE: Mexico: Michoacán: *Hinton 15325* (holotype, NY, isotype, MO).

Echites parviflora Sesse and Moç., Fl. Mex. 44. 1893. non Roxb. (1832) nec Afz. ex Ettingshausen (1861).
Prestonia caudata Woods. Ann. Missouri Bot. Gard. 47: 79. 1960. TYPE: Costa Rica: Puntarenas: *Holm and Iltis 243* (MO).

This curious plant has an equally curious taxonomic history. Its generic affinities are not at all evident; in fact, it is so unusual in Apocynaceae that I tried to refer unidentified specimens to Asclepiadaceae before I was familiar with the species. The salient characteristics are the caudately elongated corolla lobes, which are densely puberulous above; these unusual lobes and the short corolla tube give the plant a distinctly Asclepiadaceous appearance. Since its best generic assignment is to *Prestonia,* one of the Apocynaceae genera that most closely approaches Asclepiadaceae, it may well be a survivor of the ancestral plexus from which Asclepiadaceae arose.

Presumably Woodson never saw material of *Echites parviflora* Sesse and Moçiño. In his monograph of *Echites* and related genera (Ann. Missouri Bot. Gard. 23: 169–438. 1936) he listed it as an unassigned rejected species "impossible to interpret." However, two years later (North American Flora 29: 103–192. 1938) he resurrected it, reproducing the Sesse and Moçiño description, and accepting it in *Echites.* Monachino (Bull. Torrey Bot. Club 86: 245–247. 1959) realized that *E. parviflora* Sesse and Moçiño is a later homonym of *E. parviflora* Roxb. as well as of *E. parviflora* Afz. ex Ettingshausen. From the description Monachino recognized the Sesse and Moçiño plant as being conspecific with a plant collected by Hinton in Michoacán and Guerrero, Mexico, and proposed the nomen novum *E. woodsoniana* for it, substituting one of the Hinton collections as type. Meanwhile, Woodson received a Costa Rican collection of the same species and described it as an unusual species of *Prestonia,* noting that its only close relative in *Prestonia* is West Indian *P. agglutinata* (Jacq.) Woods., distinguished by similar narrowly elongate corolla lobes and exappendiculate corolla tube. Unfortunately, Woodson's description of the Costa Rican plant appeared one year later than Monachino's of the Mexican one, necessitating the new combination *Prestonia woodsoniana* (Monachino) A. Gentry, if Woodson's decision to include the species in *Prestonia* is accepted.

This species turns out to be widespread in the dry forest area along the Central American Pacific coast, ranging from Guanacaste and adjacent Puntarenas Province in Costa Rica to Guerrero and Michoacán in Mexico. There are recent collections from both Honduras and Nicaragua, as well as Costa Rica at MO. Unfortunately, the recent collections of *P. woodsoniana* have all been misidentified as *Echites tuxtlensis* Standl., a somewhat similar-looking (except for the much longer corolla tube and non-caudate corolla lobes) species from the Caribbean side of northern Central America and southern Mexico. *Echites*

woodsoniana was apparently included in *E. tuxtlensis* in the Flora of Guatemala (Fieldiana, Bot. 24(8): 334–407. 1966) as well. Presumably all Pacific coast collections of *E.* "*tuxtlensis*" are actually *Prestonia woodsoniana.*

It should be noted that my transfer of Monachino's epithet to *Prestonia* reflects no firm opinion that this species really belongs in that genus. Rather, I am merely accepting Woodson's judgement to that effect. The definitive character of *Prestonia,* the faucal annulus around the mouth of the corolla tube, is so weakly defined in *P. woodsoniana* as to be virtually non-existent. Nevertheless, the specialist in Echitoideae considered this plant best referred to *Prestonia* and I assume that that remains the best placement pending another revision of the genus.

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ALSTONIA (APOCYNACEAE): ANOTHER PALAEOTROPICAL GENUS IN CENTRAL AMERICA

Representatives of several palaeotropical genera have been discovered in Central America in recent years. So many examples of this pattern have now turned up (see Gentry, 1982: 124–125) that this disjunction is no longer surprising, if no less interesting. Presumably many of these genera with Central American range disjunctions, usually with relationships to Asian rather than to African taxa, reflect remnants of a widespread tropical Laurasian Tertiary flora (cf. Raven & Axelrod, 1974; Gentry, 1982).

While preparing a summary of Apocynaceae taxonomy for the Missouri Botanical Garden's weekly Floristic Taxonomy Seminar, I was startled to realize that the endemic Central American genus *Tonduzia* looks suspiciously similar to many species of the widespread palaeotropical genus *Alstonia.* Further study revealed that the striking resemblance is a real one and *Tonduzia* should be reduced to the synonymy of *Alstonia.* Indeed such a reduction was proposed long ago by Pichon (1947), who noted that there is nothing to distinguish *Tonduzia* from *Alstonia* and reduced it to a section of that genus. Although Pichon treated *Tonduzia* as a distinct section of *Alstonia,* it constitutes a poorly demarcated one: every one of the distinguishing features of section *Tonduzia* are shared with one of the other two sections of *Alstonia* that he recognized. That even such an inveterate generic splitter as Pichon (cf. comments in Gentry & Tomb, 1979: 756–757; Gentry, 1980: 8), who proposed two new segregate genera from *Alstonia* and resurrected two others in the same paper in which he sank *Tonduzia,* considered *Tonduzia* congeneric with *Alstonia* should have rendered the merger definitive. However, Pichon's proposal appears to have been overlooked by all subsequent workers (e.g., Standley & Williams, 1969; Nowicke, 1970; Woodson, in herb.) and *Tonduzia* is still recognized in Willis' Dictionary (Airy Shaw, 1973) and in all North American herbaria.

Pichon (1947) was aware that several species of *Tonduzia* had been described but had seen material of only the type species, *Tonduzia longifolia* (DC.) Mgf. (*T. parvifolia* Donn. Sm. is a synonym of *T. longifolia*) and refrained from proposing new combinations for the other species. Thus the only specific epithet available for a Neotropical species of *Alstonia* is *A. longifolia* (DC.) Pichon. Three species of *Tonduzia* are now accepted (Standley & Williams, 1969) necessitating the following new combinations in *Alstonia*:

Alstonia macrantha (Woods.) A. Gentry, comb. nov. *Tonduzia macrantha* Woods., Ann. Missouri Bot. Gard. 24: 12. 1937. TYPE: Guatemala. Quezaltenango: *Skutch 871* (MO).

T. longipedunculata Woods., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 78. 1944. TYPE: Guatemala. Sololá: *Steyermark 47313* (MO).

Alstonia pittieri (Donn. Sm.) A. Gentry, comb. nov. *Tonduzia pittieri* Donn. Sm., Bot. Gaz. 49: 456. 1910. TYPE: Guatemala. Guatemala: *Deam 6098* (MO).

Recognition of *A. pittieri* as specifically distinct is on rather tenuous grounds as the broader leaves and relatively high stamen insertion cited

in the Flora of Guatemala as distinguishing it from *A. longifolia* are not always associated. While additional collections are needed to resolve the status of *A. pittieri, A. macrantha* is easily recognized by its larger flowers.

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—Alwyn H. Gentry, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

THE GENUS *BOTRYARRHENA* IN VENEZUELA

Since the publication of the author's Rubiaceae of Venezuela (Steyermark, 1974), a number of new taxa of the family have been added to the flora of Venezuela. In addition to various species new to the republic, two genera of Rubiaceae, *Joosia* and *Botryarrhena*, previously unreported for Venezuela, are newly recorded. The Andean genus, *Joosia*, was collected by the author, accompanied by Ronald Liesner and Angel González, in the state of Táchira, while *Botryarrhena*, a monotypic genus, previously known only from Amazonian Brazil, was discovered by Gerrit Davidse, accompanied by Otto Huber and Stephen S. Tillett. A second, Venezuelan species of *Botryarrhena* is described here.

Ducke (1933) described *Botryarrhena* as a new genus of the subtribe Eugardenieae of the tribe Gardenieae, and believed it to be related to the genus *Retiniphyllum*, although the latter is generally relegated to a separate tribe, Retiniphylleae. The species, *B. pendula*, was stated by Ducke to resemble *Stachyarrhena penduliflora* K. Schum., another member of the tribe Gardenieae, in having simply racemose inflorescences, but otherwise differing from the genus *Stachyarrhena* in the possession of hermaphroditic instead of dioecious flowers, bilocular ovary with two ovules in each cell instead of a 4–5-celled ovary with numerous ovules in each cell, and an elongated, bilobed stigma.

A comparison of the Venezuelan collection, known only from fruiting material, with the Brazilian species, indicates that the two represent different taxa, the Venezuelan plant having short, erect infructescences with shorter, more crowded pedicels, larger leaves, and more prominently reticulate tertiary venation.

The Venezuelan collection, the second species known for the genus, may be described as follows:

Botryarrhena venezuelensis Steyermark, sp. nov.

Arbol 10-metralis; stipulis late deltoideis obtusis 4 mm longis 6 mm latis; foliis oppositis petiolatis, laminis late oblongo-oblanceolatis vel oblongo-ellipticis apice late obtusis basi cuneatim angustatis 22–30 cm longis 9–13.5 cm latis utrinque glabris, nervis lateralibus utroque latere 12–13, supra impressis subtus elevatis, venulis tertiariis utrinque prominulis valde reticulatis; petiolis 2–3 cm longis; calyce hypanthioque 3 mm longo (hypanthio 2 mm longo 2.5 mm lato glabro; calyce 1.5 mm longo 3 mm lato apice truncato paullo repando glabro); bracteola sub flore lanceolato acuto 2 mm; pedicellis fructiferis 1.5–2 mm longis; infructescentia 3–5 cm longa simplice vel prope basin semel ramosa; ovario 2-loculare, orulis in quoque loculo 2; fructibus congestis subglobosis apicem versus angustatis, apice paullo elevato truncato munitis, exocarpio 0.5 mm crasso, endocarpio glabro; seminibus subgloboso-ovalibus extremitatibus rotundatis 10 mm longis 6–8 mm latis glabris.

Tree 10 meters tall with all parts glabrous. Stipules broadly deltoid, obtuse, 4 cm long, 6 mm wide. Leaves opposite, petiolate, broadly oblong-oblanceolate to oblong-elliptic, somewhat abruptly narrowed to a broadly obtuse apex, cuneately narrowed at the base, 22–30 cm long, 9–13.5 cm wide; lateral nerves 12–13 on each

side, strongly impressed above, elevated below; tertiary venation prominently strongly reticulate. Petioles 2–3 cm long. Infructescence simple or once branched near the base, 3–5 cm long; fruiting pedicels 1.5–2 mm long, crowded on the rachis. Fruiting calyx and hypanthium 3 mm long; hypanthium 2 mm long, 2.5 mm wide; calyx truncate with a slightly repand border, 1.5 mm high, 3 mm wide. Bracteole lanceolate, acute, 2 mm long. Fruit depressed-subglobose, apically narrowed to a slightly truncate summit, 17–20 mm long, 15–17 mm wide, the base articulate with the pedicel; exocarp thin, 0.5 mm thick; endocarp thin, glabrous. Seed subglobose-oval, rounded at the ends, 10 mm long, 6–8 mm wide, glabrous. Ovary 2-celled; ovules 2 in each cell, axile.

TYPE: VENEZUELA: Terr. Fed. Amazonas: Depto. Atabapo: southeastern bank of the middle part of Caño Yagua at Cucurbital de Yagua, Lat. 3°36′N, Long. 66°34′W, alt. ca. 120 m, 8 May 1979, *G. Davidse, O. Huber & S. Tillett 17427* (VEN, holotype; MO, isotype).

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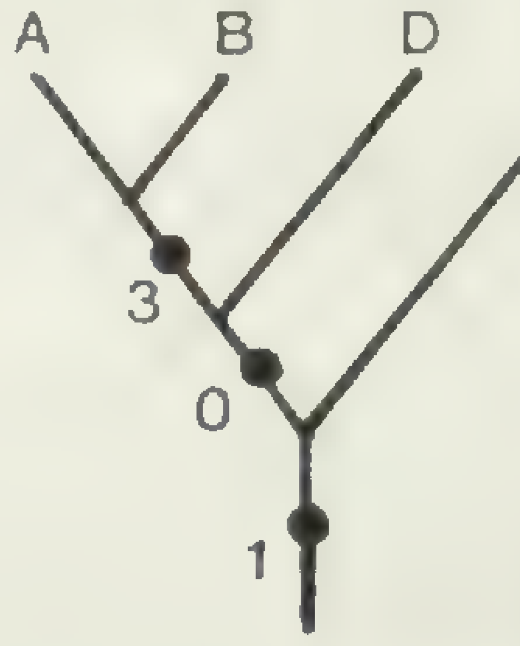
—*Julian A. Steyermark, Herbario Nacional, Caracas, Venezuela.*

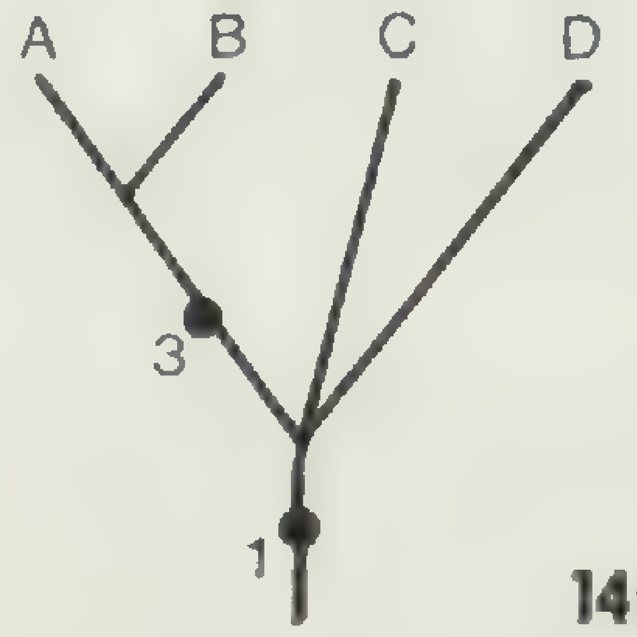
Corrigenda

The following corrections should be made in the paper titled "Vicariance biogeography in Mesoamerica," by C. J. Humphries (1982. 69: 444–463). The second sentence on page 456 should read: "Under assumption one (Fig. 13 iii–v), combining the two cladograms would give two components 0 and 3, and an informative cladogram." The last sentence in the same paragraph should read: "Combining the three cladograms together under assumption one is partially informative."

Figures 13v and 14vii shown below should replace the incorrect figures on pages 457 and 458, respectively.



13v



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The previous issue of the Annals of the Missouri Botanical Garden, Vol. 69, No. 4, pp. 735–998, was published on August 8, 1983.

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A REVISION OF THE GENUS *ANTHURIUM* (ARACEAE) OF MEXICO AND CENTRAL AMERICA. PART I: MEXICO AND MIDDLE AMERICA[1]

Thomas B. Croat[2]

Abstract

Anthurium (Araceae), a distinct neotropical genus with more than 700 species, is a member of the subfamily Pothoideae. The genus ranges from Northern Mexico and the Greater Antilles to Southern Brazil and Northern Argentina and Paraguay. Species diversity is greatest at lower to middle elevations of northern South America, Panama, and Costa Rica, while the upper Amazonian forests and lower Amazonian forests are relatively poor in species. In this paper, 122 species from Mexico and Middle America are revised. The 152 Panamanian species will be treated in a subsequent paper. In Mexico and Middle America, Costa Rica is richest in species, with 65. The remainder of Middle America is relatively poor in species, with Nicaragua having only 25 known species, Honduras having only 13 known species, Guatemala having 25 known species, and Belize fewer than 10 species. Mexico has 41 known taxa with 26 species endemic. In all, six new taxa from Mexico and Middle America were described in this revision: **A. armeniense**, **A. chamulense** Matuda ssp. **oaxacanum**, **A. halmoorei**, **A. lancetillense**, **A. nelsonii**, and **A. rzedowskii**. In addition, five new combinations have been proposed, including **A. chiapasense** ssp. **tlaxiacense** (Matuda) Croat, **A. cuneatissimum** (Engler) Croat, **A. pedatoradiatum** ssp. **helleborifolium** (Schott) Croat, **A. schlechtendalii** ssp. **jimenezii** (Matuda) Croat, and **A. subcordatum** ssp. **chlorocardium** (Standl. & L. O. Wms.) Croat.

Anthurium, a neotropical genus with more than 700 species, is a member of subfamily Pothoideae. Pothoideae contains ten genera, with only *Anthurium* and *Heteropsis* occurring in the American tropics. The Pothoideae is tropical, except for the tribe Acoreae, which contains the widespread genus *Acorus* and the Australian endemic *Gymnostachys.* The tribes Culcasieae and Zamioculcaseae with 26 species are strictly African. Four Asian genera, *Pothoidium, Anadendrum, Pothos,* and *Pedicellarum,* account for eight percent of the species of the subfamily. Only *Pothos,* with about 50 species, is very large.

Araceae contains 110 genera and more than

[1] This study was completed with support from National Science Foundation grant DEB 77-14414. The revision was based on field observations in Mexico and Central America during 1976, 1977, and 1979 and on studies in Panama since 1967. In addition, all but 12 of the 122 species are in cultivation at the Missouri Botanical Garden, and extensive observations on these living collections have been carried out. I acknowledge the assistance of D. Nicolson, who reviewed the manuscript, and of B. McAlpin, B. Virden, and H. Kamemoto, who provided critical living material. Descriptions are largely based on living collections, but descriptive data were supplemented by the extensive collections at MO and borrowed collections from A, BR, CAS, CR, F, G, H, K, M, MEXU, MICH, NY, P, UC, and US. I thank the curators of these herbaria for the loan of materials. Finally, I acknowledge the technical assistance of Frances Mazanec, Patricia Croat, Ann Ruger, and Emily Colletti.

[2] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

2,500 species. It is worldwide in distribution but has most species in tropical areas. Its centers of distribution include both Asia and America (Croat, 1979). There are 14 genera restricted to Africa, and a few genera restricted to temperate regions of the northern hemisphere, including the Mediterranean region. Important local centers of diversity include subtropical and warm temperate South America, with eleven endemic genera, and the Indomalayan region, with thirteen endemic genera. At least 1,350 species, roughly 55 percent of the total, occur in the New World tropics and subtropics. Roughly half of these are *Anthurium*.

Materials and Acknowledgments

The terminology and usage in the descriptions in this paper are defined in "Standardization of *Anthurium* Descriptions" (Croat & Bunting, 1979). Colors referenced in the descriptions that follow are taken from the color chart by Berlin and Kay (1969). This color chart, available from the University of California Press, is a reproduction of the Munsell Color Array of 40 hues, at maximum saturation, with nine degrees of brightness. The B & K (Berlin & Kay) color chart, as it is referred to here, represents 40 hues in the vertical columns and 9 degrees of brightness in the horizontal rows. Colors are arranged in 10 basic clusters with 4 different hues per cluster, ranging from red through yellow, green, blue, purple, and finally red-purple. The four columns for each color cluster are numbered 2.5, 5, 7.5, and 10. These numbers are repeated for each basic color type. The colors from the B & K color chart are read by first reporting the color, then the row followed by the column. For example, the third color in the fifth row in the red area would be called Red 5/7.5. The second color in the eighth row would be called Red 8/5. I have preceded the color references by B & K to indicate which color chart is being used.

Although a more complete discussion of flowering behavior of *Anthurium* has been published elsewhere (Croat, 1980), mention should be made here of the descriptions of flowering behavior, especially with regard to the development of stigmatic droplets and the progressive development of stamens. Most observations reported here are based on the study of cultivated material, and references to the degree of accumulation of stigmatic fluid might be inaccurate in the absence of pollinators to remove it. Nevertheless, these observations show that important taxonomic characters are exhibited by the timing and amount of stigmatic fluid and particularly by the developmental sequence of the stamens. They are therefore recorded here as part of the description of the species where they have been observed.

All estimates of ecological zones given in this paper are based on either Holdridge Life Zone maps for most Central American countries and for Panama or on the "Mapa de tipos de vegetacion de la Republica Mexicana" (Flores et al., 1971). As yet no study has been made to correlate the vegetation types represented on the Mexican map with those of the Holdridge Life Zone system. For an understanding of this system see Holdridge, et al. (1971).

Distribution of *Anthurium*

Anthurium ranges from Mexico (Tamaulipas on the Caribbean slope and Nayarit on the Pacific slope) to northern Argentina and Paraguay. Species diversity is greatest in the low and middle elevations of northern South America, Panama, and Costa Rica, with less important centers in the mountains of southern Mexico and southeastern Brazil. While the upper Amazon forests of Bolivia and especially Peru, Ecuador, and Colombia are rich in species, the lower Amazon is relatively poor in species.

Distribution of Central American *Anthurium*

Because of the large size of the genus and its taxonomic difficulty, revisionary work on *Anthurium* must progress in stages. There are approximately 219 species of *Anthurium* in Mexico and Central America (including Panama). This paper, the first of a series, will deal with 122 Mexican and Middle American taxa, but will exclude a revision of the Panamanian species, which number 152 species alone. The latter will be presented in Part II of this paper. Owing to the great morphological variability in most parts of *Anthurium*, it has been very difficult to prepare a key to large numbers of species. In addition, the Panamanian species are not yet sufficiently well known to complete a key to the species occurring in Panama. This is due to the fact that Panama has almost as many species as the rest of Central America and Mexico put together.

Most of these species have been discovered only in recent years and many are still poorly known.

The Costa Rican *Anthurium* flora is more closely related to that of Panama than to that of the remainder of Central America, but it is relatively well known (Croat & Baker, 1979), and thus will be included here.

Although Nicaragua is beginning to receive serious botanical attention as the result of the Flora of Nicaragua Project conducted by W. D. Stevens (Missouri Botanical Garden), its aroid flora is proving to be relatively poor. Most *Anthurium* species collected in Nicaragua represent species of Costa Rica and Panama that reach their limit in Nicaragua. These are found principally in the very wet southeastern corner in the Department of Zelaya. Examples of these are *A. acutangulum* Engl., *A. hacumense* Engl., *A. ochranthum* C. Koch, *A. ramonense* Engl. ex K. Krause, *A. spathiphyllum* N. E. Brown, and *A. upalaense* Croat & Baker. Other species are basically Mexican species that just reach Nicaragua from the north. Examples of these are *A. huixtlense* Matuda and *A. schlechtendalii* Kunth.

Additional Nicaraguan *Anthurium* species include wide ranging species that range from Mexico or Middle America to South America, such as *A. cubense* Engl. (also in West Indies), *A. clavigerum* Poepp., *A. friedrichsthalii* Schott, *A. gracile* (Rudge) Lindl., *A. interruptum* Sodiro, *A. microspadix* Schott, *A. obtusilobum* Schott, *A. ravenii* Croat & Baker, *A. scandens* (Aubl.) Engl., and *A. trinerve* Miq. Still others are species that range throughout Central America, such as *A. bakeri* Hook. f. and *A. pentaphyllum* (Aubl.) G. Don var. *bombacifolium* (Schott) Madison. These are also expected to be found in Colombia. The only endemic species of *Anthurium* known from Nicaragua is *A. beltianum* Standl. & L. O. Wms.

To date, only 25 species are known for Nicaragua and, although it is certain that more species will be added to the flora with the ongoing collecting by Stevens and his associates, there is little doubt that species diversity of *Anthurium* is greater south of the San Juan depression, which separates Costa Rica and Nicaragua. Costa Rica, although appreciably smaller, has approximately 65 species of *Anthurium* (Croat & Baker, 1979). Panama is even richer with 152 species. Nicaraguan forests that I have investigated were poor in species. For example, the cloud forest on Volcán Mombacho east of Lake Nicaragua had only a few species of aroids. Even the much wetter cloud forest regions between Jinotega and Matagalpa produced relatively few species. In a comparable cloud forest of Costa Rica or Panama, many species can be encountered in a small area.

The remainder of Middle America is, like Nicaragua, relatively poor in species. Honduras has only 13 known species with an additional four species, namely *A. friedrichsthalii* Schott, *A. microspadix* Schott, *A. schlechtendalii* Kunth, and *A. trinerve* Miq., expected there. Like Nicaragua, Honduras is expected to have only a single endemic species, namely *A. lancetillense* Croat.

Belize has no more than eight to ten species (none of them endemic) but Guatemala, with about 25 species, is richer.

Although the greater number of species in Guatemala can perhaps be attributed in part to the fact that it has been much better explored than the remainder of Middle America, the chief reason for its greater number of known species is that it shares with Mexico a number of typically Mexican species. These include *A. chiapasense* Standl., *A. huixtlense* Matuda, *A. montanum* Hemsl., *A. seleri* Engl., and *A. titanium* Standl. & Steyerm. A number of other species from Chiapas are to be expected in Guatemala. These include *A. berriozabalense* Matuda, *A. chamulense* Matuda, *A. cordatotriangulum* Matuda, *A. nakamurae* Matuda, *A. ovandense* Matuda, and *A. pedatoradiatum* Schott.

Still, Guatemala is much richer in species in its own right than the remainder of Middle America, with three endemic species. These are *A. armeniense* Croat, *A. parvispathum* Hemsl., and *A. retiferum* Standl. & Steyerm. However, all of these might possibly also be discovered in Chiapas with further collecting there.

Mexico, with 41 known taxa and an additional four or five species to be expected, has a relatively rich *Anthurium* flora with 26 endemic taxa. Some of the endemic taxa are relatively widespread within Mexico, such as *A. andicola* Liebm., *A. chiapasense* Standl., *A. schlechtendalii* ssp. *jimenezii* (Matuda) Croat, *A. nizandense* Matuda, *A. ovandense* Matuda, *A. pedatoradiatum* Schott, and *A. podophyllum* (Cham. & Schlecht.) Kunth. The majority, however, are relatively narrow endemics, mostly known only from northern Oaxaca (seven taxa, *A. cerropelonense* Matuda, *A. chamulense* ssp. *oaxacanum* Croat, *A. longipeltatum* Matuda, *A. machetioides* Matuda, *A. nelsonii* Croat, *A. subovatum* Matuda, *A. umbrosum*

Liebm., *A. yetlense* Matuda); northern Chiapas (four taxa, *A. berriozabalense* Matuda, *A. clarinervium* Matuda, *A. leuconeurum* Lem., *A. lezamae* Matuda); or southeastern Chiapas (two taxa, *A. cordatotriangulum* Matuda, *A. nakamurae* Matuda).

Many of the Mexican species appear closely related, and their current isolation is perhaps due to changes in the environment brought about by increasingly arid conditions and the formation of broad expanses of intervening desert or extremely arid areas. Thus, for example, *A. halmoorei* Croat, *A. schlechtendalii* ssp. *jimenezii* (Matuda) Croat, and *A. nizandense* Matuda all appear to have been derived from *A. schlechtendalii* Kunth, a common species from the Caribbean slope (or from a common ancestor). Speciation here would appear to have resulted from the onset of arid conditions with the resulting isolation of these species in specific parts of western Mexico. Similar isolation of species has occurred in Chiapas, where relatively close species are now endemic to northern Chiapas or to southeastern and southwestern Chiapas.

That Mexico and Middle America were isolated from Costa Rica and Panama during the evolution of many Mexican *Anthurium* species seems obvious from the fact that only six Mexican species, including *A. flexile* Schott, *A. microspadix* Schott, *A. pentaphyllum* var. *bombacifolium* (Schott) Madison, *A. salviniae* Hemsl., *A. scandens* (Aubl.) Engl., and *A. trinerve* Miq., reach Costa Rica. The same six species extend also to Panama and the latter two range throughout much of South America as well. The situation in Guatemala is little better with only ten species reaching Costa Rica. These include (in addition to the Mexican species already mentioned) *A. bakeri* Hook. f., *A. cubense* Engl., *A. gracile* (Rudge) Lindl., and *A. interruptum* Sodiro. The three latter species are also present in South America.

Further evidence of this isolation can be seen in the distinctive nature of many Mexican species and the predominance of D-shaped or broadly sulcate petioles that are uncommon elsewhere in *Anthurium*. This feature is exhibited in several leaf forms, including species with oblong leaf blades and ovate-cordate blades, as well as in pedatisect species, such as *A. podophyllum* (Cham. & Schlecht.) Kunth and *A. pedatoradiatum* Schott. The Mexican species in this group will be referred to as the *Anthurium andicola* alliance. They may ultimately prove to be a section in their own right, but final judgment on this will be deferred until further work can be done with the South American species of the genus.

History of Work with Central American *Anthurium*

The last revision of *Anthurium* was that of Engler (1905), who reported 58 species for Central America. The work was completed at a time before serious botanical activity had begun in many parts of Central America, and the number of species is now estimated at 219, almost a fourfold increase.

Since Engler's time, most work conducted on *Anthurium* in Central America has been the piecemeal description of new species and the compilation of floras for Guatemala, Costa Rica, and Panama. Most of the treatments were prepared by P. C. Standley, who also made a substantial number of collections. The Flora of Guatemala treatment was completed by P. C. Standley and J. A. Steyermark (1958). Steyermark also made many collections, especially in Guatemala, and must be mentioned as one of the few collectors who paid any attention to descriptive detail of the plants in his notes.

The most serious student of *Anthurium* was Eizi Matuda, who, over the course of approximately 30 years (beginning about 1949), worked with the Araceae of Mexico. In all, Matuda described 36 species (many of these now in synonymy) of *Anthurium* from Mexico. Matuda played an important role in botanizing in Mexico, especially in Chiapas. Several of the species he collected and described have not been seen since. Matuda's most important work (1954) summarized the Araceae flora of Mexico as it was known then, but he also described a number of species after the publication of that revision.

Also important in the study of Mexican Araceae was G. S. Bunting, whose "Commentary on Mexican Araceae," published in 1965, summarized his knowledge gained from four extensive field trips to Mexico during 1959, 1961, and 1962. Some of his commentary was useful in preparing my own field trips to Mexico. A revision of the palmately-lobed species of *Anthurium* by M. Madison (1978) has also been useful during the preparation of this revision.

Only 35 of the 122 species inhabiting Mexico and Middle America were described before Engler's time. Of these, the largest number (19 species) were described by Schott with lesser

numbers by Hemsley (three species), Poeppig and Endlicher (two species), Masters (two species), and Liebmann (two species). The remaining seven species were each published by a different author: Hooker, Rudge, Lemaire, Chamisso & Schlechtendal, Aublet, Kunth, and Miquel.

Engler published an additional thirteen species near the turn of the century and Luis Sodiro, working in Ecuador, described two Central American species that range there during the same period.

Matuda, leading the list of *Anthurium* workers subsequent to Engler's time, published 19 species. Standley and his co-workers, L. O. Williams and J. A. Steyermark, published five species as a result of their work with the floristics of Central America. A single species each was described by J. F. Macbride, T. G. Yuncker, and L. H. Bailey during the same general period. Recently described material includes 20 species by Croat and Baker (1979) and a single taxon each by R. Sheffer and G. M. Barroso. This paper will describe six additional new species.

Several people, although not describers of *Anthurium*, nevertheless made significant contributions by means of their collecting efforts. These include D. Breedlove (Chiapas), R. Baker and W. C. Burger (Costa Rica), H. Kennedy (Mexico and Central America), T. MacDougall (Mexico especially Oaxaca), and D. Neill and W. D. Stevens (Nicaragua). Special mention should be made regarding collections of Thomas MacDougall because he had the unusual practice of recollecting a species in the same area. When he did, he frequently (if not always) assigned the recollected plant the same number he had assigned it originally, using only a different date to distinguish different specimens. This practice has led in several cases to mixed collections when his later collections were in fact a different species that occurred in the same area.

Taxonomic Characters

Morphological characters used in the taxonomy of *Anthurium* depend to some extent upon the section being dealt with, but the characters that have been used most frequently have been shape and venation of the leaves, internode length, and the color and shape of the spathe and spadix. Many of these characters are already discussed elsewhere (Croat & Bunting, 1979).

Roots. Although roots have not been used traditionally as taxonomic characters, they display a wide variety of qualitative characters. Typically, roots develop one or more at each node. In section *Polyphyllium* Engl., the roots are numerous, short, and slender and are borne along the internodes. In most species of section *Pachyneurium* Schott, and in other short-stemmed species as well, the roots per node are much more numerous. Since the internodes are very short, the root mass can be large and dense, with the roots contiguous or nearly so. In many cases, there has been a divergence in the function of roots so that some are utilized exclusively for support while others are negatively geotropic and are directed upward where they collect debris, or they extend into the rosette of leaves and collect debris. In other cases, the support roots of the plant are negatively geotropic, such as in the case of pendent species (Madison, 1978). Commonly, roots appear smooth when fresh; when they are dry it can be seen that they actually consist of a dense mass of woolly trichomes that are so closely matted they look contiguous before shrinkage of the root. *Anthurium gracile* (Rudge) Lindl. has roots with a thick white layer of velamen useful in absorption of moisture from the air. Other species that have been investigated lack this velamen layer.

Stems and cataphylls. Although stem anatomy has not been adequately studied, the outward appearance of the stem provides few good taxonomic characters except for a considerable range in length and width of the internodes. Stems are usually scurfy and brown in age. While there is a considerable difference in the size, shape, and degree of indentation of the petiole scars, these characters have not been used systematically.

Much more important are the cataphylls that frequently persist on the stem. The color, texture, and the degree of weathering they undergo are useful taxonomic characters. Growth in *Anthurium* is sympodial with each shoot bearing a bicarinate prophyll and a larger, single-keeled cataphyll, a foliage leaf, and terminating in an inflorescence. The inflorescence, although always potential, may abort (Engler, 1877). The cataphylls, which are usually green, promptly turn brownish, reddish, or yellowish and may be deciduous. More frequently they persist, either remaining intact, such as in section *Calomystrium* Schott and some other species, or they are marcescent, variously weathering into a network of persistent fibers that may accumulate debris. The

color, degree of weathering, and degree of persistence of the cataphylls frequently provide useful taxonomic characters.

Leaves. Among the more useful taxonomic characters that have been overlooked previously is the cross-sectional shape of petioles (Fig. 1). Most *Anthurium* species have petioles that are terete or subterete in cross-section and frequently also narrowly and obtusely channelled. However, considerable variation exists, and at least sometimes this is believed to be taxonomically significant. Many Mexican species have petioles that are D-shaped or broadly sulcate in cross-section. Petiole cross-sectional shape, within limits, has proven useful in the separation of species of *Anthurium* in the section *Pachyneurium* Schott, where leaf blades of many of the bird's-nest species are otherwise almost identical. However, petiole shape cannot be relied on entirely. Some of the more variable, wide-ranging species, such as *A. schlechtendalii* Kunth, have considerable variation in petiole cross-sectional shape even within a single population (see that species for a discussion of this). Some species of *Anthurium* have sharply triangular petioles, others trapezoidal, square, or terete with several to many sharp ridges. The degree of channelling of the petiole also provides useful taxonomic characters. The length of petioles, like overall size of any morphological part of *Anthurium*, is highly unreliable because plants often flower when quite young and thus the overall size of leaves, inflorescences, and other parts vary remarkably in size over the course of the life of the plant. More useful is the relative length of the petiole in comparison to the length of the inflorescence.

The most widely used taxonomic characters in *Anthurium* are the shape and venation of the leaves, since these are perhaps more diverse than in any other genus of plants (Croat & Bunting, 1979). In addition, glandular punctations on the leaf blades provide useful characters and are valid, at least sometimes, at the sectional level. For example, sections *Porphyrochitonium* Schott, *Tetraspermium* Schott, and *Digitinervium* Sodiro consistently have glandular punctations on one or both surfaces. Still, some species in otherwise epunctate sections, such as section *Calomystrium* Schott, have evolved glandular punctations independently. While many members of section *Calomystrium* Schott have brownish spots resembling the glandular punctations of section *Porphyrochitonium* Schott and others, at least one unknown isolated Brazilian species (*Rosa & Lira 2325*) has definite glandular punctations on the lower blade surface. A group of coriaceous, cordate species from Mexico (*A. verapazense* alliance) has also developed glandular punctations.

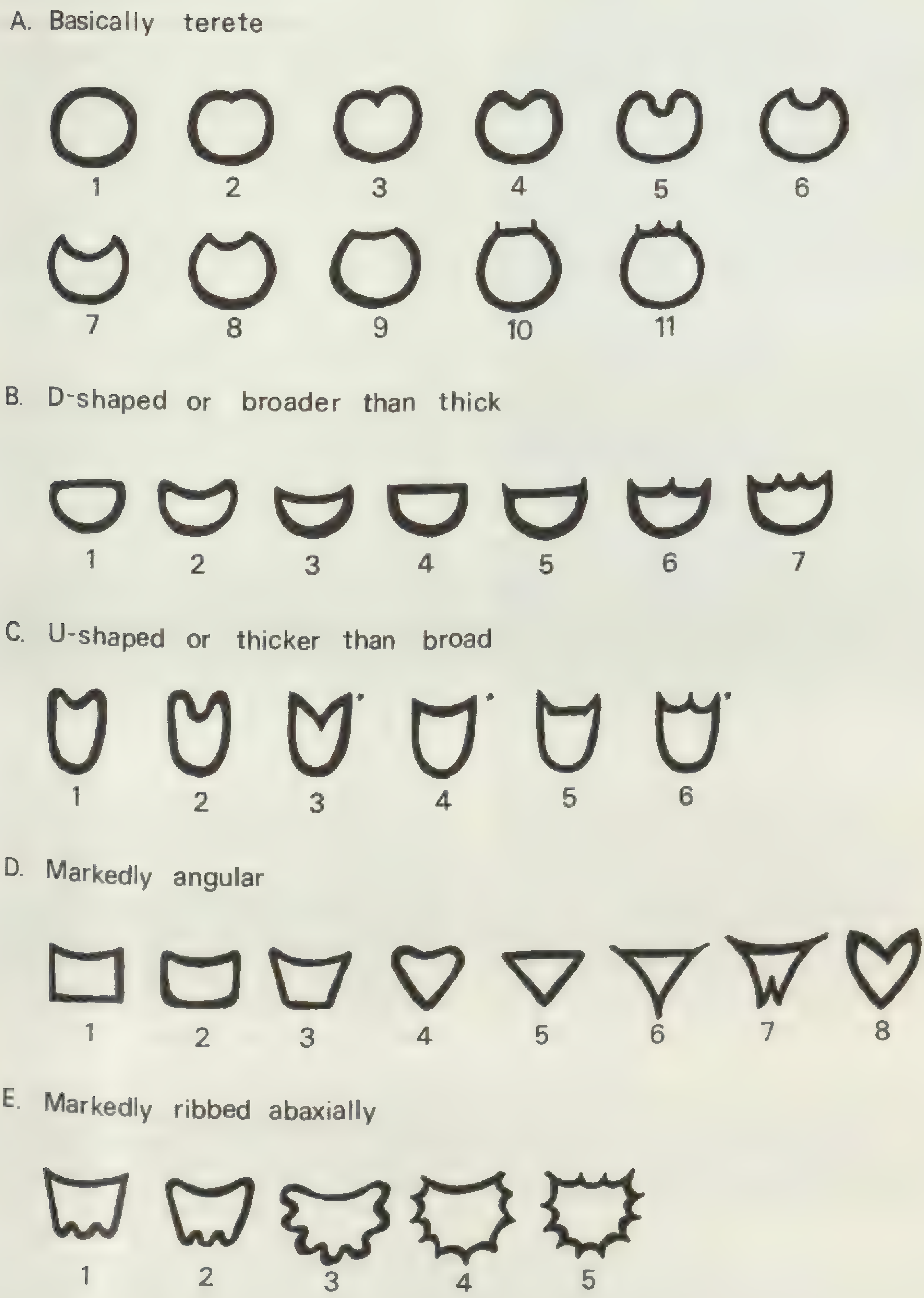
Other useful features in the leaf include the presence of papillate epidermal cells, such as in section *Cardiolonchium* Schott, and the presence of easily visible raphide cells so prevalent in section *Calomystrium* Schott.

Inflorescences. The inflorescence, although generally critical for identification of species of *Anthurium*, has been under utilized, perhaps be-

FIGURE 1. Cross-sectional petiole shapes in *Anthurium*.—A. Basically terete: ranging from esulcate (1), to shallowly and acutely sulcate (2 & 3), to obtusely and broadly sulcate (4), to narrowly and obtusely sulcate (5), to narrowly and acutely sulcate (6), broadly and acutely sulcate (7), shallowly and broadly sulcate (8), flat adaxially (9), flat adaxially with marginal ribs (10), to flat adaxially with marginal and medial ribs (11).—B. D-Shaped or broader than thick: ranging from flat adaxially with obtuse margins (1), to broadly sulcate with obtuse margins (2), broadly sulcate with acute margins (3), flat adaxially with acute margins (4), flat adaxially with erect margins (5), flat adaxially with erect margins and with 1 or more medial ribs (6 & 7).—C. U-shaped or thicker than broad: ranging from broadly and obtusely sulcate (1) to narrowly and obtusely sulcate (2), narrowly and acutely sulcate with acute margins* (3), shallowly and acutely sulcate* (4), sulcate with acute margins (5), sulcate with sharp margins and a medial rib* (6).—D. Markedly angular: ranging from quadrangular with acute angles (1) to quadrangular with obtuse angles (2), trapezoidal (3), obtusely triangular (4), acutely triangular (5), acutely triangular with two marginal ribs (6), basically triangular with two abaxial ribs (7), obtusely triangular, narrowly and sharply sulcate with convex sides (8).—E. Markedly ribbed abaxially: ranging from trapezoidal or quadrangular, sharply and broadly sulcate adaxially, 3-ribbed abaxially (1), to obtusely and broadly sulcate adaxially, 3-ribbed abaxially (2), broadly and obtusely sulcate adaxially 5-ribbed abaxially (3), broadly and sharply sulcate adaxially, narrowly and sharply ribbed around the remaining circumference (4), or with one or more ribs on the sulcus (5).

* Not yet observed but to be expected.

CROSS-SECTIONAL PETIOLE SHAPES IN ANTHURIUM



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cause of too much reliance on herbarium material, which greatly diminished the value of the inflorescence. Peduncle length has frequently been used as a taxonomic character, yet length alone is extremely variable on plants of different ages and even in populations of plants of the same age. However, the ratio of the peduncle length to the petiole length is usually relatively constant and often provides a useful character. Like most vegetative parts, the overall dimensions of the spathe and spadix are not very useful, but again the ratio of the length of the spathe to the length of the spadix is relatively reliable. The shape of both the spathe and spadix and the texture of the spathe are usually much more reliable than size.

The spadix and the many characters it embodies is perhaps one of the least used taxonomically. This is no doubt due to the fact that too few species have been critically compared in live condition. The dried spadix is difficult to study and loses many of the characters that are apparent before drying. One of the most useful characters exhibited by the spadix is color. Spadix color when seen at anthesis is usually stable, and species vary considerably in the colors exhibited. In some species, however, the spadix varies from green to violet-purple. While many spadices are green before the spathe opens, most quickly assume the color they will have at anthesis. Some species may be green when stamens begin to emerge and later may turn violet-purple. Some species change colors after anthesis, so it is important to make note of the color at anthesis. *Anthurium huixtlense* Matuda and *A. formosum* Schott, for example, have spadices that become noticeably darker after anthesis.

Other characters exhibited by the spadix include scent, size, shape, and texture of the flowers; the number of flower spirals and the number of flowers per spiral; the disposition of the stigmas and timing of the stigmatic droplets; the rate of emergence and disposition of the stamens, as well as the shape of anthers and pollen color. Many of these characters are discussed in detail in Croat (1980), but a summary of the important points will be included here as well.

Although there has been no success as yet in determining scents of flowering *Anthurium*, there is little doubt that a large percentage of them have distinctive aromas. Those with attractive bright spadices have sweet aromas, such as of mint or lilac, and are no doubt bee-pollinated. Euglossine bees have been seen in several cases visiting *Anthurium* (Croat, 1980). Species with purple or drab colored spadices generally have yeasty or rotting fruit aromas (the scent of one species is like that of fresh cucumbers) and are probably fly-pollinated. Scents are usually not evident at night, and some species are phenologically active, presenting their aromas only during midday. Aromas of some species are sometimes so intense as to be smelled easily from a distance of several meters, but most species give only faint but distinct aromas.

Flowers are closely aggregated in spirals and are quite variable in size and shape. Their overall shape at the apex may be square, rhombic, or 4-lobed. The tepals themselves may be 3, 4, or 5-sided. The texture of the surface, presence of droplets, raphide cells, and other features, all may be taxonomically important.

Stigmas may be slitlike or brushlike and exserted. The production of stigmatic droplets varies considerably from species to species, with both timing and duration being important. The sequence and duration of stamens as well as their method of presentation is similarly important. While most anthers are merely exserted just above the tepals, the stamens in some species are exserted and later the filament shrinks and retracts the anther to the surface of the tepals. Stamens in other species do not retract and the filament and anthers remain exposed. Stamens in still others retract completely below the surface of the tepals and thus out of sight. The sequence of staminal emergence is also quite variable (Croat, 1980), with the rate of emergence being an additional variable. Most species with typically long-tapered spadices have emergence beginning at the base of the spadix and progressing toward the apex. Species with cylindroid or clavate spadices have staminal emergence generally scattered or even beginning at the apex or middle. In all types of spadices the rate of emergence may be quite different. For example some species develop all of their lateral stamens before the third (alternate) stamen and finally the fourth (alternate) stamen emerge. Still other species have all stamens of the flowers in any spiral fully exserted before many flowers in succeeding spirals have their lateral stamens exserted. In other words, the leading spirals in the staminal development progression are few. In contrast, other species may have, for example, ten or more of the leading spirals with only lateral stamens exposed, with another ten or more of the preceding spirals bearing three stamens (i.e., the laterals plus the third, usually anterior, stamen) and finally all of

the lower (basal) spirals with a full complement of four stamens exposed.

All of the characters mentioned here have proven to be useful taxonomic characters, yet most have never been mentioned previously by other workers.

Fruits. *Anthurium* fruits consist of 2-loculed berries. The berries provide a number of useful characters including size, shape, and color, the nature of the pericarp and mesocarp, the presence or absence of raphide cells, as well as the number, size, and shape of seeds. Engler (1905) appeared to realize the significance of the berries in classification, but unfortunately he had not seen berries on the majority of the species he studied. Because *Anthurium* has markedly protogynous flowers (Croat, 1980), they do not readily set fruit on greenhouse collections without manipulation. Often this is not possible without a second individual of the species. A great deal of attention has been given to those species in the living collections for which fruits were not known, in order to encourage them to set fruit.

The number of seeds per locule has long been considered an important character, with such groups as sections *Tetraspermium* Schott, *Gymnopodium* Engl., and *Porphyrochitonium* Schott having more than one seed per locule, while the remaining sections usually have one per locule.

Seeds themselves are as individually different from species to species as are the berries. Most have sticky, mucilaginous appendages firmly associated with them (Croat, 1980) often attached to one or both ends. In some cases the seed is completely enclosed in a mucilaginous envelope. These extremely sticky structures seem ideally suited to being attached to bird beaks, and *Anthurium* berries seem ideally suited for bird dispersal. Many of the Mexican species of *Anthurium* lack a sticky appendage on the seeds.

Sectional Classification of Central American *Anthurium*

In many cases the existing sectional classification systems of Schott and of Engler are inadequate. While some species assigned to various sections by Engler (1905) may be related, most sectional descriptions have many overlapping characteristics, and I believe that many species assigned to a particular section by Engler bear little relationship to each other, e.g., *A. gracile* (Rudge) Lindl. and *A. friedrichsthalii* Schott in Schott's section *Leptanthurium*, and *A. protensum* Schott and *A. durandii* Engl. in Engler's section *Urospadix*. *Anthurium friedrichsthalii* Schott is a typical member of section *Porphyrochitonium* Schott, as is *A. durandii* Engl., while *A. protensum* Schott is a member of section *Pachyneurium* Schott.

A review of the sectional classification of *Anthurium* will be published elsewhere and, although an attempt will eventually be made to revise the sectional classification of *Anthurium*, it is premature to arrange Central American species in any subgeneric classification system in this treatment. An attempt will be made here, however, tentatively to assign all Central American species to a section. In some cases species will be placed within an alliance of species that may later be ranked at the sectional level.

It is hoped that ongoing studies with live material including cytological, anatomical, and chemical studies will prove adequate to provide a thorough analysis of the sectional classification of the genus.

Provisional Sectional Placement of *Anthurium* Species of Mexico and Middle America*

1a. Leaf blades prominently 3-lobed or palmatifid to palmatisect.
  2a. Leaf blades with the lobes united at the base.
    3a. Leaf blades with three lobes (the lateral or posterior lobes often smaller than the central lobe) .... Section *Semaeophyllium* Schott

A. subsignatum Schott
A. tilaranense Standl.

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* Three sections do not occur in Central America: section *Gymnopodium* Engl. is represented by a single species *A. gymnopus* Griseb. from Cuba; section *Chamaerepium* Schott, represented by a single species *A. radicans* C. Koch & A. Haage, is restricted to Brazil; section *Urospadix* Engl. may be restricted to South America and is concentrated in eastern and southeastern Brazil. Some Panamanian species are tentatively placed in section *Urospadix*.

3b. Leaf blades with five or more lobes. .... Section *Schizoplacium* Schott
A. pedatoradiatum Schott
A. pedatoradiatum ssp. *helleborifolium* (Schott) Croat
A. podophyllum (Cham. & Schlecht.) Kunth

2b. Leaf blades with the lobes free to the base. .... Section *Dactylophyllium* Schott
A. clavigerum Poepp.
A. kunthii Poepp.
A. pentaphyllum (Aubl.) G. Don var. *bombacifolium* (Schott) Madison
A. trisectum Sodiro

1b. Leaf blades entire or nearly so, sometimes with the anterior lobe markedly constricted at the base but never distinctly 3-lobed.

4a. Leaf blades conspicuously dark glandular-punctate at least on the lower surface.

5a. Leaf blades cordate, hastate, or otherwise with usually definite posterior lobes; most basal veins usually merging with the margin of the blade proximal to the middle of the blade. .... Section *Belolonchium* Schott (*Anthurium verapazense* alliance)
A. chiapasense Standl.
A. chiapasense ssp. *tlaxiacense* (Matuda) Croat
A. longipeltatum Matuda
A. lucens Standl. ex Yuncker
A. riograndicolum Matuda
A. verapazense Engl.

5b. Leaf blades acute to obtuse or subcordate at base with usually only a single collective vein extending along the margin to the apex (Sections *Tetraspermium* and *Porphyrochitonium*) or with several basal veins prominently arcuate-ascending to the apex with many close, parallel primary lateral veins extending between all the basal veins giving the blade the appearance of a melastomataceous leaf blade (Section *Digitinervium*).

6a. Leaf blades with several pairs of basal veins sharply arcuate-ascending, extending to or almost to the apex; primary lateral veins numerous, distinct, parallel, and extending more or less straight between all the basal veins, giving the leaf blade the appearance of a melastomataceous blade; pistils often prominently exserted and quadrangular; number of ovules and seeds per locule unknown. .... Section *Digitinervium* Sodiro
A. lentii Croat & Baker

6b. Leaf blades with usually no more than one pair of basal veins (usually merely the collective vein) extending along the margin to the apex; primary lateral veins usually not numerous or closely parallel; pistils not quadrangular; ovules and seeds usually two or more per locule.

7a. Plants mostly scandent; stems slender, mostly less than 6 mm diam.; internodes somewhat elongate; acute at apex. .... Section *Tetraspermium* Schott
A. scandens (Aubl.) Engl.
A. scandens ssp. *pusillum* Sheffer
A. tonduzii Engl.
A. trinerve Miq.

7b. Plants usually more or less caespitose, at least lacking slender scandent stems; stems usually more than 1 cm diam.; berries often more or less truncate and indented at the apex. .... Section *Porphyrochitonium* Schott
A. acutangulum Engl.
A. alatipedunculatum Croat & Baker
A. austinsmithii Croat & Baker
A. bakeri Hook. f.
A. durandii Engl.
A. friedrichsthalii Schott
A. hacumense Engl.
A. lancifolium Schott
A. louisii Croat & Baker
A. paludosum Engl.
A. ramonense Engl.
A. scherzerianum Schott
A. utleyi Croat & Baker
A. wendlingeri G. M. Barroso

4b. Leaf blades epunctate or at least not conspicuously dark glandular-punctate.

8a. Petioles D-shaped in cross-section or broadly channelled with more or less acute lateral margins. .... Section *Belolonchium* Schott (*Anthurium andicola* alliance)
A. andicola Liebm.
A. berriozabalense Matuda

A. cerrobaulense Matuda
A. chamulense Matuda
A. chamulense ssp. *oaxacanum* Croat
A. cordatotriangulum Matuda
A. cotobrusii Croat & Baker
A. montanum Hemsl.
A. nakamurae Matuda
A. nelsonii Croat
A. parvispathum Hemsl.
A. retiferum Standl. & Steyerm.
A. rionegrense Matuda
A. rzedowskii Croat
A. seleri Engl.
A. subcordatum Schott
A. subcordatum ssp. *chlorocardium* (Standl. & L. O. Wms.) Croat
A. subovatum Matuda
A. titanium Standl. & Steyerm.

8b. Petioles usually terete or subterete in cross-section often narrowly channelled but with the margins rounded; sometimes square, triangular, trapezoidal, or otherwise, but not usually D-shaped.

9a. Vernation of leaf blades involute (i.e., with both margins rolled inward toward the midrib in bud); plants frequently with a "bird's-nest" habit, i.e., short stems and rosulate leaves; blades often thick, frequently more or less oblanceolate or obovate to elliptic; the primary lateral veins (at least the lower ones) joining the margins. .... Section *Pachyneurium* Schott

A. acutifolium Engl.
A. brenesii Croat & Baker
A. consobrinum Schott
A. cubense Engl.
A. cuneatissimum (Engl.) Croat
A. cuspidatum Mast.
A. eximium Engl.
A. fatoense K. Krause
A. halmoorei Croat
A. machetioides Matuda
A. michelii Guillaumin
A. nizandense Matuda
A. oerstedianum Schott
A. prolatum Croat & Baker
A. protensum Schott
A. purpureospathum Croat
A. ranchoanum Engl.
A. salvadorense Croat
A. salviniae Hemsl.
A. schlechtendalii Kunth
A. schlechtendalii ssp. *jimenezii* (Matuda) Croat
A. schottianum Croat & Baker
A. seibertii Croat & Baker
A. spathiphyllum N. E. Brown
A. spectabile Schott
A. standleyi Croat & Baker
A. upalaense Croat & Baker
A. validifolium K. Krause
A. watermaliense Hort. ex L. H. Bailey

9b. Vernation of leaf blades supervolute (i.e., with one margin rolled inward toward the midrib but with the alternate margin rolled around the midrib and then rolled up opposite margin, giving the "cut-away" view a cochleate appearance); plants usually lacking a bird's-nest habit; leaves various; the primary lateral veins frequently joining into a collective vein before reaching the margin.

10a. Stems scandent and wiry; internodes elongate, usually less than 3 mm thick, with numerous, short adventitious roots scattered along their length; flowering branches bearing one to six leaves; 1-ribbed cataphylls lacking. ...... Section *Polyphyllium* Engl.

A. clidemioides Standl.
A. flexile Schott
A. flexile ssp. *muelleri* (Macbr.) Croat & Baker

10b. Stems short or scandent but not slender and wiry; internodes short or long but not

slender and wiry, usually more than 8 mm diam.; the adventitious roots restricted to the nodes; flowering branches bearing a single leaf (branches are short and do not appear like branches); 1-ribbed cataphylls present and usually conspicuous.

11a. Roots white, bearing velamen; blades thin, narrowly oblanceolate, the primary lateral veins numerous and scarcely more prominent than the interprimary veins,* stems rarely more than 1 cm diam. with persistent reddish-brown, intact cataphylls; spadix with no more than three flowers visible per spiral (from any angle); chromosome numbers $2n = 10$ or 20. .... Section *Leptanthurium* Schott

A. gracile (Rudge) Lindl.

11b. Roots usually greenish, lacking velamen; blades various, usually with the primary lateral veins conspicuously more prominent than the interprimary veins; stems various; cataphylls usually weathering (except section *Calomystrium* with cordate blades); number of flowers per spiral various but usually more than three per spiral.

12a. Leaf blades velvety, usually metallic green or blackish-green in color; the epidermal cells papillate or otherwise elevated; petioles frequently ribbed; B-chromosomes present. .... Section *Cardiolonchium* Schott

A. clarinervium Matuda
A. leuconeurum Lem.
A. lezamae Matuda

12b. Leaf blades not velvety, usually smooth and semiglossy to glossy; the epidermal cells flat, not papillate or raised; petioles various but not commonly ribbed; B-chromosomes lacking.

13a. Stems bearing conspicuous, thick, intact, persistent, reddish-brown cataphylls; leaf blades usually thick; the minor veins usually not prominently raised; the upper blade surface usually with linear raphide cells visible; spadix often colored, often sweetly scented; spathe usually thick, often broad. .... Section *Calomystrium* Schott

A. armeniense Croat
A. beltianum Standl. & L. O. Wms.
A. clavatum Croat & Baker
A. formosum Schott
A. hoffmannii Schott
A. huixtlense Matuda
A. monteverdense Croat & Baker
A. obtusilobum Croat & Baker
A. ravenii Croat & Baker

13b. Stems usually with cataphylls deciduous or weathering into a mass of fibers (sometimes persisting intact, as in *A. eximium*); leaf blades thick or thin; the minor veins conspicuous or not; the upper surface usually lacking raphide cells; spadix various, less frequently scented; spathe various, often lanceolate.

14a. Leaf blades much longer than broad, oblong to linear (rarely ovate but then thin, veiny, and weakly bullate as in *A. davidsoniae*).

15a. Stems elongate, erect to scandent 7–20 mm diam.

16a. Leaf blades thin, veiny, and weakly bullate: the reticulate veins often conspicuous; spathe and spadix usually green or greenish-yellow; spadices commonly cylindrical; berries commonly pale green. .... Section *Xialophyllium* Schott

(*A. microspadix* alliance)
A. davidsoniae Standl.
A. microspadix Schott
A. pallens Schott

16b. Leaf blades usually coriaceous or thickly chartaceous, smooth; the reticulate veins usually not conspicuous; spathe and spadix various or not known. .... Section *Xialophyllium* Schott

(*A. caucanum* alliance)

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* Section *Urospadix* centered in Brazil and apparently not represented in Central America have leaf blades that also have this characteristic.

A. angustispadix Croat & Baker
A. burgeri Croat & Baker
A. carnosum Croat & Baker
A. interruptum Sodiro
A. tenerum Engl.
A. testaceum Croat & Baker

15b. Stems short; the internodes short; stems mostly less than 10 mm diam.
17a. Pistils prominently exserted long before anthesis and many times longer than the stamens when they appear. .... Section *Oxycarpium* Schott
A. pittieri Engl.
A. pittieri var. *fogdenii* Croat
17b. Pistils not prominently exserted long before anthesis, about as long or no more than a few times longer than stamens. .... Section *Xialophyllium* Schott
A. burgeri Croat & Baker (usually with longer stems)

14b. Leaf blades not much longer than broad (or at least not oblong or linear), mostly more or less ovate with posterior lobes.
18a. Blades moderately thin, often conspicuously veiny or even bullate; anterior lobe usually with numerous, close, more or less parallel veins; berries frequently green. .... Section *Polyneurium* Schott
A. caperatum Croat & Baker
A. panduriforme Schott
A. williamsii K. Krause
18b. Blades coriaceous or nearly so, usually smooth and not noticeably veiny or bullate; anterior lobe lacking numerous close parallel veins. .... Section *Belolonchium* Schott
A. brownii Mast.
A. cerropelonense Matuda
A. concinnatum Schott
A. lancetillense Croat
A. ochranthum C. Koch
A. ovandense Matuda
A. pluricostatum Croat & Baker
A. silvigaudens Standl. & Steyerm.
A. umbrosum Liebm.
A. yetlense Matuda

Key to *Anthurium* of Mexico and Middle America

1a. Leaves palmately lobed or divided; leaf segments more than three or if three, then divided to the base. .... KEY A
1b. Leaves simple, sometimes lobed.
2a. Leaf blades 3-lobed, the margins constricted near the base of the anterior lobe. .... KEY B
2b. Leaf blades not 3-lobed.
3a. Leaf blades cordate or subcordate at base.
4a. Leaf blades with prominent posterior lobes, conspicuously black punctate below. .... KEY C
4b. Leaf blades with posterior lobes, not punctate below or not conspicuously so. .... KEY D
3b. Leaf blades not cordate or subcordate at base.
5a. Leaves punctate on one or both surfaces. .... KEY E
5b. Leaves not punctate on either surface. .... KEY F

Key A

Leaves palmately lobed or divided; leaf segments more than three or if three, then divided to the base.

1a. Leaves 3-foliolate with the segments free to the base; plants terrestrial. .... *A. trisectum* Sodiro
1b. Leaves 5–13-foliolate or lobed (if 3-foliolate, then the peduncle less than 5 cm long).
2a. Blade segments all free to the base.
3a. Plants huge, scandent, epiphytic; leaflets lobed; peduncle elongate; spadix to 75 cm long; spathe dark violet-purple. .... *A. clavigerum* Poepp.
3b. Plants relatively small, scandent, with long internodes; leaflets not lobed (except the basal leaflet); peduncle long or short; spadix less than 25 cm long; spathe green to purplish.

4a. Leaf segments all more or less equal, petiolules 4–6 cm long; peduncles slender and long, usually more than 20 cm long, longer than spadix; spadix whitish to greenish at anthesis. .... *A. kunthii* Poepp.
4b. Leaf segments unequal, the lowermost more or less auriculate and usually markedly inequilateral; petiolules usually short, less than 2 cm long with the leaf tissue decurrent, often almost to the base; peduncles short and stout, usually less than 6 cm long, usually shorter than the spadix; spadix lavender at anthesis. .... *A. pentaphyllum* var. *bombacifolium* (Schott) Madison
2b. Blade segments united at the base; plants terrestrial or on rocks on steep slopes.
5a. Blade segments generally pinnatifid with 5–12 narrow divisions, the segments rarely entire but then subcoriaceous; the peduncle longer than the petioles. .... *A. podophyllum* (Cham. & Schlecht.) Kunth
5b. Blade segments entire, the peduncle shorter than the petioles.
6a. Blades evenly segmented. .... *A. pedatoradiatum* Schott ssp. *pedatoradiatum*
6b. Blades unevenly divided, at least the median segment free or nearly so. .... *A. pedatoradiatum* ssp. *helleborifolium* (Schott) Croat

KEY B

Leaves simple, 3-lobed, the margins constricted near the base of the anterior lobe.

1a. Posterior lobes usually more or less orbicular; lower blade surface glossy, yellow-green when dry; primary lateral veins numerous, prominent, more or less straight and parallel; tepals yellow. .... *A. panduriforme* Schott
1b. Posterior lobes not as above; lower blade surface not glossy; primary lateral veins either not numerous or not prominent or neither; tepals purple or yellow to green.
2a. Basal lobes at more or less right angles to the anterior lobe.
3a. Plants scandent with long internodes; spadix yellow-green to yellow; berries violet-purple. .... *A. subsignatum* Schott
3b. Plants more or less acaulescent with short internodes; spadix neither yellow-green nor yellow; berries red or violet-purple.
4a. Posterior lobes curved toward anterior lobe; spadix creamy-white or greenish to reddish-brown; berries red, at least at apex. .... *A. tilaranense* Standl.
4b. Posterior lobes extended away from anterior lobe; spadix green tinged with violet-purple; berries violet-purple. .... *A. seleri* Engl.
2b. Basal lobes not at more or less right angles to anterior lobe.
5a. Posterior lobes broadly rounded, the sinus usually spathulate; spadix violet-purple; blade margin often undulate; Costa Rica to Ecuador. .... *A. brownii* Mast.
5b. Posterior lobes narrow, the sinus not spathulate; spadix usually greenish; blade margins not markedly undulate; Mexico and Guatemala.
6a. Blades with the posterior lobes usually longer than the anterior lobe; the margin between the anterior and posterior lobes straight to convex; the collective vein arising usually from the uppermost basal vein in the anterior lobe. .... *A. berriozabalense* Matuda
6b. Blades with the posterior lobes usually shorter or no longer than the anterior lobe; the margin between the anterior and posterior lobes usually markedly concave; the collective vein arising from one of the lowermost basal veins and extending along the margin of both the posterior and the anterior lobes. .... *A. seleri* Engl.

KEY C

Leaves simple, cordate, or subcordate at base; with prominent posterior lobes, black punctate below.

1a. Leaf blades usually subcordate, stiffly coriaceous with two or more basal veins strongly ascending, roughly parallel to the midrib to beyond the middle of the blade; pistils early emergent, quadrangular in cross-section; berries white; Costa Rica, Panama, Colombia. .... *A. lentii* Croat & Baker
1b. Leaf blades usually conspicuously lobed at the base, subcoriaceous, the basal veins not as above, usually forming a collective vein near the margin, usually only the uppermost extending above the middle of the blade; pistils not markedly early emergent, terete in cross-section; berries red, orange, or purplish at maturity.
2a. Blades mostly 2–3 times longer than broad, the anterior lobe usually more or less oblong and sometimes constricted at the base or narrowly triangular.
3a. Posterior lobes mostly less than 1.25 times longer than broad, the sinus parabolic to spathulate, often closed; northern Oaxaca in the Sierra Madre Oriental. .... *A. longipeltatum* Matuda
3b. Posterior lobes mostly more than 1.5 times longer than broad, usually directed prominently outward; the sinus campanulate to spathulate, not closed; southern Oaxaca and Chiapas to Belize, Guatemala and Honduras.
4a. Inflorescences usually 1.5–3 times longer than the petioles; berries subglobose, red-orange to orange-red; seeds 6–9 per berry, less than 3 mm long. .... *A. verapazense* Engl.

4b. Inflorescences usually less than 1.5 times longer than petioles.
5a. Spadix olive green at anthesis; primary lateral veins prominently raised below (fresh and dry); restricted to southwestern Oaxaca. .... *A. chiapasense* ssp. *tlaxiacense* (Matuda) Croat
5b. Spadix dark violet-purple at anthesis; primary lateral veins flat or prominulous below; southeastern Chiapas and western Guatemala. ... *A. chiapasense* Standl. ssp. *chiapasense*
2b. Blades mostly 1.25–1.5 times longer than broad, rarely more than 2 times longer than broad, the anterior lobe usually more or less ovate (rarely with the anterior lobe somewhat oblong or narrowly triangular).
6a. Blades conspicuously coriaceous, acute at the apex with a short apiculum; southeastern Oaxaca. .... *A. riograndicolum* Matuda
6b. Blades usually only subcoriaceous (at least when dry), acuminate at apex; widespread from Chiapas to Honduras.
7a. Inflorescences usually 1.5–3 times longer than petioles; spathe usually less than half as long as the spadix; berries subglobose, red-orange to orange-red; seeds 3–5 per locule (7–9 per berry), less than 3 mm long. .... *A. verapazense* Engl.
7b. Inflorescence usually less than 1.5 times as long as the petioles; spathe usually more than half as long as spadix; berries obovoid, bright red; seeds 1 per locule (2 per berry), more than 4.5 mm long. .... *A. lucens* Standl. ex Yuncker

KEY D

Leaves simple, cordate or subcordate at base, with posterior lobes, epunctate below.

1a. Plants scandent and twining or at least with long slender stems with elongate internodes, held erect usually by rooting onto or being supported by trees; blades mostly less than 27 cm long.
2a. Leaves bullate; peduncle nearly non-existent, obscured by the base of spathe, rarely to 5 cm. .... *A. clidemioides* Standl.
2b. Leaves not bullate (except *A. davidsoniae*); peduncles conspicuous.
3a. Stems mostly more than 2 cm diam.; blades 16–48 cm long, 11–44 cm wide. .... *A. subsignatum* Schott
3b. Stems mostly less than 1 cm diam.; blades mostly less than 27 cm long, 16 cm wide.
4a. Stems 2–4 mm diam., usually several meters long, twining, flexible; internodes with many short roots; sea level to 1,700 m.
5a. Leaves usually palminerved, lanceolate, cordate at base and broadest below the middle of the blade; spadix usually with a conspicuous stipe 1–2 cm long; Mexico to northern Guatemala, 1,000–1,700 m. .... *A. flexile* ssp. *muelleri* (Macbr.) Croat & Baker
5b. Leaves plinerved, elliptic to narrowly elliptic, narrowly subcordate at base, broadest at or near the middle of the blade; spadix sessile or with the stipe to 2 mm long; Mexico to Panama, sea level to 1,000 m. .... *A. flexile* Schott ssp. *flexile*
4b. Stems usually 5–10 mm diam., usually 1 m or less long, usually stiffly erect, usually supported by a tree, not twining, the internodes lacking roots; roots long, few, restricted to the nodes; usually 1,200–2,300 m.
6a. Leaf blades all cordate or, rarely, subcordate. .... *A. davidsoniae* Standl.
6b. Leaf blades subcordate intermixed with blades that are rounded or truncate, rarely cordate. .... *A. microspadix* Schott
1b. Plants not scandent; internodes short.
7a. Species of Costa Rica and Panama, often extending into South America, sometimes into Nicaragua (*A. ravenii* as far north as Honduras).
8a. Geniculum situated at least 10 cm below the base of the blade; blades subcordate; terrestrial. .... *A. oerstedianum* Schott
8b. Geniculum immediately subtending the leaf blade.
9a. Spadix more or less clavate, broader in circumference at apex than at base; spathe ovate-elliptic with a long-cuspidate apex, long-decurrent at base; blades drying dark brown or gray-brown; middle elevations, Cordillera de Talamanca. .... *A. clavatum* Croat & Baker
9b. Spadix cylindroid or tapering from base to apex, never clavate; spathe mostly oblong, lanceolate, or ovate.
10a. Spathe purple to dark maroon or mottled green and purple throughout (excluded are species with spathe predominantly green with purple tinged margins and/or veins).
11a. Spathe twisted and contorted; peduncle short (less than 20 cm), dwarfed by the elongate petioles (to 1 m long); sinus narrow; Atlantic lowlands near Bribrí, 100 m. .... *A. schottianum* Croat & Baker
11b. Spathes flat; peduncles more than 20 cm long, or if shorter, not dwarfed by the petioles; sinus narrow or broad; mostly 400–2,400 m.
12a. Leaf blades shallowly cordate or subcordate at base; spathe solid maroon

to more commonly green and purple mottled; leaves basically lanceolate in outline.

13a. Leaf blades thin; spadix sessile, berries purple-violet becoming red; major veins of leaf reddish beneath on drying. .... *A. cuspidatum* Mast.

13b. Leaf blades subcoriaceous; spadix on a stipe 3–25 mm long; berries orange; major veins of leaf not reddish beneath. .... *A. ranchoanum* Engl.

12a. Leaf blades deeply cordate at base or shallowly cordate and triangular in outline.

14a. Spathe usually dark purple-violet; stipe 0.5–2.5 cm long; stamens long-exserted. .... *A. watermaliense* Hort. ex L. H. Bailey

14b. Spathe usually green tinged with purple; stipe 2–6 mm long; stamens weakly exserted. .... *A. cotobrusii* Croat & Baker

10b. Spathe white, yellow, green, or green with purple-tinged veins and/or margins.

15a. Leaf blades generally lanceolate or broadly lanceolate in outline, cordate or subcordate basally, the lobes never overlapping each other; spathe green or green tinged with purple, never white.

16a. Petiole 4-sided; blades pendent; peduncle less than 25 cm long, much shorter than the petioles. .... *A. spectabile* Schott

16b. Petioles terete or subterete; blades not pendent; peduncles usually more than 25 cm long, slightly shorter to longer than petioles.

17a. Spathe oblong-lanceolate; berries purple-violet to reddish-violet; major veins of leaf maroon below; blades almost always drying with a purplish tint or with purplish blotches; 400–1,700 m. .... *A. cuspidatum* Mast.

17b. Spathe lanceolate to ovate; berries orange; major veins of leaf not maroon below; blades not drying purplish or with purplish blotches; (500)1,000–2,300 m. .... *A. ranchoanum* Engl.

15b. Leaf blades generally heart-shaped in outline, with conspicuous and deep basal sinus, the lobes often overlapping each other; spathe white, green or green tinged with purple.

18a. Blades hastate, the posterior lobes usually orbicular; spadix golden yellow. .... *A. panduriforme* Schott

18b. Blades not hastate, the posterior lobes not orbicular; spadix white, green, purple, or occasionally yellow.

19a. Plants growing at elevations above 2,000 m; flowering spadix 5–26 cm long, on a stipe 1–2.5 cm long. .... *A. concinnatum* Schott

19b. Plants usually growing at elevations below 2,000 m; spadix various lengths, usually sessile (*A. standleyi* with a stipe 0.6–6 cm long.

20a. Largest leaf blades less than 55 cm long.

21a. Spadix dark purple; spathe dark green, sometimes tinged purple.

22a. Blades subcoriaceous, the basal veins coalesced 4–6 cm, the sinus much broader than deep when flattened; spathe ovate to narrow; berries pale orange. .... *A. cotobrusii* Croat & Baker

22b. Blades thin, the basal veins scarcely or not at all coalesced, the sinus much deeper than broad, sometimes closed with the lobes overlapping; spathe lanceolate; berries deep red-violet. .... *A. williamsii* K. Krause

21b. Spadix white to yellow or pale green, sometimes tinged purplish.

23a. Collective vein continuous from near base of basal lobe to apex of blade. .... *A. obtusilobum* Schott

23b. Collective vein formed only in upper half of blade, arising from upper basal veins, the lower basal veins running to margin.

24a. Blades ovate-triangular, the sides of the anterior lobe nearly straight; cataphylls weathering into tan fibers; spathe usually purple, at least tinged purplish; plants terrestrial. .... *A. watermaliense* Hort. ex L. H. Bailey

24b. Blades ovate, the sides convex; cataphylls

persisting more or less intact, reddish-brown; spathe pale, not tinged purplish plants epiphytic or terrestrial.

25a. Spathe 5–6(8.5) cm wide, broadly ovate. .... *A. monteverdense* Croat & Baker

25b. Spathe less than 3 cm wide, lanceolate to oblong-ovate. .... *A. hoffmannii* Schott

20b. Largest leaf blades more than 55 cm long.

26a. Leaf blades with tertiary veins sunken above, giving the blade a bullate appearance, drying pale yellow-green with a wrinkled, chartaceous character; submarginal collective vein usually continuous from near the base; spathe pale green, brittle; spadix pale green; berries pale green or white. .... *A. caperatum* Croat & Baker

26b. Leaf blades not appearing bullate; submarginal collective vein often beginning well above base; spathe color various, often tinged purplish; spadix white, yellow, purple, or green tinged with purple; berries orange, reddish, or purplish.

27a. Plants epiphytic.

28a. Spadix violet-purple, long tapered, to 28 cm long; blade prominently undulate. .... *A. brownii* Mast.

28b. Spadix white, pale green, greenish-yellow, or violet, short and only slightly tapered, to 18 cm long.

29a. Spathe soon reflexed; spadix cream, white or pale yellow-green; berries red, round at apex. .... *A. ravenii* Croat & Baker

29b. Spathe remaining close to spadix even in fruit; spadix white to violet; berries dark purple-violet with red-orange base, sharp pointed at apex. .... *A. formosum* Schott

27b. Plants terrestrial.

30a. Collective vein arising well above the middle; spathe green; spadix green when immature, soon heavily tinged violet-purple, turning yellow-brown; berries orange. .... *A. standleyi* Croat & Baker

30b. Collective vein usually arising from one of the basal veins; spathe white, pale green or pale violet or tinged with pale violet; spadix white, yellow, lavender, or pale green tinged with lavender; berries not orange.

31a. Blades usually drying with large, conspicuous, purplish blotches; spathe pale green becoming pale violet; spadix white to violet; berries dark purple-violet with red-orange base; common plants of the Atlantic slopes at middle elevations, sometimes seen as the dominant plant on disturbed steep banks. .... *A. formosum* Schott

31b. Blades lacking dark splotches; spathe and spadix various colors; berries not colored as above.

32a. Spadix bright yellow at anthesis, the anthers not visible (pollen oozing out in slender ribbons); leaf blades with the posterior lobes elongated, the

anterior lobe usually somewhat straight along its margins; petiole rounded and smooth abaxially. .... *A. ochranthum* C. Koch

32b. Spadix pale lavender or green tinged with lavender; anthers clearly visible, held just above the tepals; leaf blades with posterior lobes scarcely longer than broad; anterior lobe usually broadly convex along its margins; petiole subterete with seven or eight low ridges around its circumference. .... *A. pluricostatum* Croat & Baker

7b. Species of Mexico and northwestern middle America, northwest of Río San Juan depression (Nicaragua), sometimes in El Salvador and Honduras, rarely in Nicaragua.

33a. Petioles broadly sulcate or D-shaped in cross-section, the adaxial margins often acute, sometimes merely obtuse.

34a. Leaf blades merely subcordate, lacking well developed posterior lobes.

35a. Leaf blades with the basal veins and primary lateral veins usually reddish; Sierra de Oaxaca in northern Oaxaca. .... *A. subovatum* Matuda

35b. Leaf blades with all veins greenish; Guerrero and southern Oaxaca to Chiapas, Guatemala, El Salvador, or Honduras.

36a. Blades less than 12 cm long; southwestern Chiapas near border with Oaxaca. .... *A. cerrobaulense* Matuda

36b. Blades usually more than 15 cm long; Oaxaca, Chiapas, Guerrero in Mexico, Guatemala, Honduras, or El Salvador.

37a. Collective vein arising from one of the lower basal veins; posterior lobes usually longer than broad and directed prominently outward; northern Chiapas to Guatemala. .... *A. seleri* Engl.

37b. Collective vein arising from the first (or second) basal vein or one of the primary lateral veins, the posterior lobes usually not longer than broad and not directed prominently outward.

38a. Blades more or less oblong, three to four times longer than broad, often broader near the base. .... *A. nakamurae* Matuda

38b. Blades triangular to ovate, less than three times longer than broad, broadest at base.

39a. Leaf blades with margins of the anterior lobe usually concave. .... *A. cerrobaulense* Matuda

39b. Leaf blade with margins of the anterior lobe broadly convex.

40a. Spadix pale green; blades with the collective vein often arising from the first basal vein, frequently with a secondary collective vein extending irregularly along the margin to the apex or nearly to the apex; second basal vein merging with the margin in the upper half of the blade; Mexico, in Guerrero and southern Oaxaca and Chiapas. .... *A. rzedowskii* Croat

40b. Spadix dark violet-purple or green tinged with violet-purple; blades with the collective vein arising from the first or second basal vein, lacking a secondary collective vein; the second basal vein often merging with the margin below the middle of the blade; Oaxaca and Chiapas, Guatemala, El Salvador, and Honduras.

41a. Leaf blades with tertiary veins obscure above (fresh); western Guatemala to northern El Salvador and western Honduras. .... *A. chamulense* Matuda, *A. subcordatum* Schott, *A. subcordatum* ssp. *chlorocardium* (Standl. & L. O. Wms.) Croat, *A. subovatum* Matuda

41b. Leaf blades with tertiary veins minutely sunk-

en and visible above when fresh; Oaxaca and Chiapas.

42a. Leaf blades with tertiary veins below scarcely visible; blades subcoriaceous; occurring in "bosque pin-encino" (see Flores, et al., 1971). .... *A. chamulense* Matuda ssp. *chamulense*

42b. Leaf blades with the tertiary veins clearly visible below; blades of medium thickness; occurring in "selva alta perennifolia." .... *A. chamulense* ssp. *oaxacanum* Croat

43a. Spathe ovate to narrowly ovate; berries orange (?); Honduras on Cerro Santa Bárbara (Dept. Santa Bárbara). .... *A. subcordatum* ssp. *chlorocardium* (Standl. & L. O. Wms.) Croat

43b. Spathe lanceolate (rarely narrowly ovate); berries bright red; western Guatemala to El Salvador and Honduras along the Continental Divide. .... *A. subcordatum* Schott ssp. *subcordatum*

34b. Leaf blades with conspicuous, well developed posterior lobes.

44a. Blades about as broad as long.

45a. Leaf blades whitish-matte beneath; north central Oaxaca. .... *A. nelsonii* Croat

45b. Leaf blades not whitish beneath.

46a. Tertiary veins prominently raised even on fresh leaves; leaf blades usually less than 40 cm long; Veracruz and Oaxaca. .... *A. andicola* Liebm.

46b. Tertiary veins not prominently raised on fresh material, weakly prominulous on drying; leaf blades variable in size; southeastern Chiapas and Guatemala.

47a. Blades less than 25 cm long, thin. .... *A. rionegrense* Matuda

47b. Blades more than 40 cm long, subcoriaceous. .... *A. titanium* Standl. & Steyerm.

44b. Blades substantially longer than broad.

48a. Lower blade surface matte, drying whitish; north central Oaxaca. .... *A. nelsonii* Croat

48b. Lower blade surface not conspicuously matte and whitish.

49a. Blade with the anterior lobe conspicuously concave along the margin; southwestern Chiapas. .... *A. cerrobaulense* Matuda

49b. Blade with the anterior lobe usually convex along the margin.

50a. Blades with the tertiary veins prominently raised even on fresh leaves; Veracruz and Oaxaca. .... *A. andicola* Liebm.

50b. Blades with the tertiary veins not prominently raised on fresh leaves, weakly prominulous on drying.

51a. Blades ovate-triangular (ovate in *A. subcordatum*), the posterior lobes poorly developed, usually rounded, the collective vein always arising from the first basal vein, the second basal vein only rarely loop-connected to the collective vein, usually merging with the margin well below the middle of the blade, the sinus usually broad, usually parabolic or arcuate; northern and southeastern Chiapas and northern Oaxaca.

52a. Blades ovate-triangular.

53a. Major veins of the blade and apex of the petiole reddish; Sierra de Juárez in northern Oaxaca. .... *A. subovatum* Matuda

53b. Major veins of the blade and the apex of the petiole green; northern and southeastern Chiapas. .... *A. chamulense* Matuda ssp. *chamulense*

52b. Blades ovate.

54a. Spathe ovate to narrowly ovate; berries or-

ange (?); Honduras on Cerro Santa Bárbara (Dept. Santa Bárbara). .... *A. subcordatum* ssp. *chlorocardium* (Standl. & L. O. Wms.) Croat

54b. Spathe lanceolate (rarely narrowly ovate); berries bright red; western Guatemala to El Salvador and Honduras along the Continental Divide. .... *A. subcordatum* Schott ssp. *subcordatum*

51b. Blades ovate to narrowly ovate or ovate-triangular; posterior lobes usually well developed, often longer than broad (except in *A. rzedowskii*), often curved inward; collective vein sometimes arising from one of the primary lateral veins, the second basal vein often loop-connected to the collective vein, usually merging with the margin well above the middle of the blade, the sinus hippocrepiform to spathulate, sometimes parabolic, rarely arcuate; Guerrero, Oaxaca or southeastern Chiapas to Guatemala.

55a. Blades coriaceous, the margins not markedly undulate; petioles not glaucous; frequently with a secondary collective vein extending irregularly along the margin to the apex or nearly to the apex; Guerrero, Oaxaca, and Chiapas. .... *A. rzedowskii* Croat

55b. Blades subcoriaceous to medium thick, usually markedly undulate (except *A. titanium*); petioles usually glaucous.

56a. Blades broadly ovate to rounded in outline, the margin of the anterior lobe convex; spadix usually more than 17 cm long. .... *A. titanium* Standl. & Steyerm.

56b. Blades ovate-triangular to narrowly ovate, the margins of the anterior lobe more or less straight; spadix usually less than 20 cm long.

57a. Blades ovate-triangular; major veins of the lower surface prominently elevated when dry; spathe lanceolate, usually about as long as the spadix; southeastern Chiapas. .... *A. cordatotriangulum* Matuda

57b. Blades broadly to narrowly ovate; major veins of the lower surface not prominently elevated on drying; spathe ovate, usually much shorter than the spadix; southeastern Chiapas to Guatemala. .... *A. montanum* Hemsl.

33b. Petioles terete or subterete.

58a. Peduncles usually less than one-third as long as longest petioles.

59a. Spadix dark purple.

60a. Leaves coriaceous, glossy; endemic to Sierra de Juárez, 2,400–2,800 m. .... *A. cerropelonense* Matuda

60b. Leaves subcoriaceous, semiglossy; Lancetilla Valley, ca. 300 m. .... *A. lancetillense* Croat

59b. Spadix green, white or lavender; leaves subcoriaceous.

61a. Spadix green; cataphylls dilacerating; peduncle less than 10 cm long; endemic to Central Guatemala, 1,500–2,000 m or to northern Oaxaca, 600–1,500 m.

62a. Spathe broadly lanceolate, more than 2.5 times longer than broad, rounded to acute at the base; spadix more than 5 times longer than broad, markedly tapered toward the apex; endemic to northern Oaxaca. .... *A. yetlense* Matuda

62b. Spathe broadly ovate, less than 1.5 times longer than broad, usually cordate at the base; spadix less than 4 times longer than broad, scarcely tapered toward the apex; endemic to central Guatemala. .... *A. silvigaudens* Standl. & Steyerm.

61b. Spadix white to lavender; cataphylls remaining intact; peduncles 21–39 cm long; Chiapas to Nicaragua. .... *A. huixtlense* Matuda

58b. Peduncles more than half as long as longest petioles.

63a. Upper blade surface papillate (with the epidermal cells cone-like) or alveolate; fresh leaves usually conspicuously velvety; Mexico.

64a. Leaf blades with veins conspicuously paler than the surface; primary lateral veins not conspicuously more prominent when dry than the interprimary and tertiary veins; epidermal cells of leaf blade drying minutely alveolate (honey-combed). .... *A. lezamae* Matuda

64b. Leaf blades with veins conspicuously paler than the blade surface; primary lateral veins conspicuously more prominent when dry than the interprimary and tertiary veins; epidermal cells obviously papillate with individual cells obviously raised, cone-like.

65a. Leaf blades almost as broad as long, the sinus closed or very narrow; basal veins free or, if united into a posterior rib, the rib not marginal to the sinus. .... *A. clarinervium* Matuda

65b. Leaf blades conspicuously longer than broad, the sinus obovate or hippocrepiform; basal veins united into a conspicuous, naked (i.e., marginal to the sinus) posterior rib. .... *A. leuconeurum* Lem.

63b. Upper blade surface smooth, not minutely papillate (the epidermal cells not raised and cone-like) or alveolate (with a raised, net-like reticulum); fresh leaves glossy or matte but not velvety; Mexico and Middle America.

66a. Posterior lobes longer than the anterior lobe. .... *A. berriozabalense* Matuda

66b. Posterior lobes not longer than the anterior lobe.

67a. Cataphylls remaining intact, usually reddish-brown, conspicuous; leaf blades with raphide cells usually visible on upper surface.

68a. Spadix at anthesis with the tepals turned upward on the inner margin to give the spadix a distinctly bumpy surface, the color pale reddish-violet, the stipe usually conspicuous, often curved, the spathe ovate-oblong, white; southwestern Guatemala. .... *A. armeniense* Croat

68b. Spadix at anthesis with tepals not conspicuously upturned, the spadix relatively smooth, rose-violet to lavender or cream, the stipe absent or short, not both elongate and curved; widespread from Chiapas to western Nicaragua. .... *A. huixtlense* Matuda

67b. Cataphylls usually weathering into fibers or deciduous; leaf blades usually lacking raphide cells.

69a. Inflorescences nodding with spathe hooding spadix; endemic to Nicaragua on limestone outcrops. .... *A. beltianum* Standl. & L. O. Wms.

69b. Inflorescences not typically nodding with spathe hooding spadix.

70a. Plants occurring above 2,000 m elevation.

71a. Second pair of basal veins (counting from the midrib) joining leaf margins below the middle of the blade.

72a. Sinus of leaf broad, shallow, arcuate; petioles not glaucous; leaf margins not undulate; blade coriaceous; principally northern Chiapas. .... *A. chamulense* Matuda

72b. Sinus usually narrow, deep, hippocrepiform to parabolic; petioles glaucous; blades subcoriaceous with undulate margins; southeastern Chiapas to Guatemala. .... *A. montanum* Hemsl.

71b. Second pair of basal veins joining leaf margin well above middle of leaf blade.

73a. Leaf blades broadly ovate, nearly as broad as long; spadix dark purple at anthesis; endemic to Sierra de Juárez in northern Oaxaca, 2,400–2,800 m. .... *A. cerropelonense* Matuda

73b. Leaf blades narrowly ovate to ovate or ovate-triangular, longer than broad; spadix green or green tinged with purple.

74a. Petioles glaucous; sinus usually spathulate to hippocrepiform, rarely parabolic; southeastern Oaxaca to Guatemala, 1,200–2,900 m. .... *A. montanum* Hemsl.

74b. Petioles not glaucous; sinus usually arcuate to parabolic, rarely spathulate; Guerrero, northern Oaxaca and Chiapas, 1,400–2,900 m. ..... *A. rzedowskii* Croat

70b. Plants occurring below 2,000 m.

75a. Leaf blades not coriaceous.

76a. Leaf blades ovate-triangular, nearly as broad as long; rare, known only from an area near the border of Oaxaca and Chiapas. .... *A. rionegrense* Matuda

76b. Leaf blades ovate, longer than broad.

77a. Spadix green at anthesis, sometimes tinged with purple; petioles weakly glaucous (except *A. rzedowskii*).

78a. Blades frequently with a secondary collective vein extending irregularly along the margin to the apex or nearly to the apex; Guerrero, Oaxaca, and Chiapas. .... *A. rzedowskii* Croat

78b. Blades lacking a secondary collective vein extending irregularly along the margin to the apex or nearly to the apex; Guerrero, Oaxaca, and Chiapas.

79a. Leaf blades with margins flat to broadly undulate; southeastern Chiapas and southwestern Guatemala, 1,200–2,900 m. .... *A. montanum* Hemsl.

79b. Leaf blades with margins minutely undulate to subcrispate; endemic to southern Oaxaca and Chiapas, 800–1,600 m. .... *A. ovandense* Matuda

77b. Spadix dark purple at anthesis; petioles usually not glaucous.

80a. Inflorescences noticeably shorter than the leaves; Honduras, near sea level. .... *A. lancetillense* Croat

80b. Inflorescences nearly as long as or longer than leaves; Mexico and Guatemala, 800–2,900 m.

81a. Leaf margins flat to slightly undulate, the anterior lobe with its margins straight to slightly convex; northern Oaxaca, 1,200–1,800 m. .... *A. umbrosum* Liebm.

81b. Leaf margins usually markedly undulate; anterior lobe with at least one margin often concave; southwestern Chiapas to Guatemala. 1,200–2,900 m. .... *A. montanum* Hemsl.

75b. Leaf blades coriaceous.

82a. Collective vein arising from one of the lower basal veins, extending along margin from near apex of posterior lobe to apex of anterior lobe; eastern Mexico to central Chiapas to west central Guatemala, 700–1,900 m. ..... *A. seleri* Engl.

82b. Collective vein arising from one of the upper basal veins, usually extending along only part

of the margin of the anterior lobe, sometimes loop-connected to lower basal veins.

83a. Sinus relatively shallow, usually arcuate with posterior lobes relatively short, never narrow; southeastern Chiapas to Oaxaca, 1,500–3,000 m. .... *A. chamulense* Matuda

83b. Sinus deep, spathulate to hippocrepiform or parabolic, the posterior lobes often elongate, sometimes longer than broad.

84a. Posterior lobes (at least on well developed leaves) elongate, two or more times longer than broad; anterior lobe usually markedly concave; petioles not glaucous; southwestern Chiapas. .... *A. cerrobaulense* Matuda

84b. Posterior lobes broadly rounded to elongate but less than 1.5 times longer than broad; anterior lobe convex to sometimes weakly concave; petioles weakly glaucous; southeastern Chiapas to south central Guatemala. .... *A. montanum* Hemsl.

KEY E

Leaves simple, not lobed; blades neither cordate nor subcordate, punctate on one or both surfaces.

1a. Spadix coiled or spiralled.

2a. Spathe showy, red to red-orange, ovate; leaf blades narrowly elliptic. .... *A. scherzerianum* Schott

2b. Spathe not showy, reddish or green tinged purplish, linear or lanceolate-oblong; leaf blades oblong or ovate.

3a. Leaf blades oblong, to 80(150) cm long. .... *A. wendlingeri* G. M. Barroso

3b. Leaf blades ovate, to 20 cm long. .... *A. louisii* Croat & Baker

1b. Spadix not coiled or spiralled.

4a. Stipe 3–20 cm long; leaf blades oblanceolate; spadix pale violet-purple. .... *A. hacumense* Engl.

4b. Stipe less than 1 cm long (usually the spadix sessile).

5a. Submarginal collective vein markedly impressed above, raised below and significantly more prominent than the primary lateral veins; berries bright red; leaves narrowly elliptic to narrowly oblanceolate, the apex acuminate. .... *A. bakeri* Hook. f.

5b. Submarginal collective vein equally as prominent as the primary lateral veins; berries pale violet, white, yellow-orange or rarely red; leaves of various shapes.

6a. Plants slender, scandent, with persisting, dilacerating cataphylls enclosing the internodes (except *A. tonduzii* with cataphylls entire, not dilacerating, deciduous); plants with long slender stems, often hanging from trees; berries translucent white or pale violet or purple; blades usually much less than 14 cm long.

7a. Internodes 2–21 cm long, not clothed in persistent cataphylls; leaf blades usually rounded at base; primary lateral veins usually three to six per side. .... *A. tonduzii* Engl.

7b. Internodes usually less than 2 cm long, rarely more than 4 cm long, at least the younger stems clothed in persistent, dilacerated cataphylls; leaf blades usually obtuse to acute at base; primary lateral veins usually numerous.

8a. Flowering spadix purplish, the pistil whitish, noticeably quadrangular, emerging prominently before stamens emerge; spathe persistently erect and more or less parallel to the spadix; berries broadly ovate to obovate, usually acute to apiculate at apex; plants growing at elevations from 0 to 800 m. .... *A. trinerve* Miq.

8b. Flowering spadix greenish, the pistil greenish, round to weakly quadrangular, emerging only after the stamens have opened; spathe strongly reflexed soon after opening; berries depressed-globose to globose, rounded to flat at apex; plants growing at elevations from 0 to 2,700 m.

9a. Spadix 16–60 flowered, 11–30 mm long at anthesis; blade punctate or not on upper surface, 4–16 cm long. .... *A. scandens* (Aubl.) Engl. ssp. *scandens*

9b. Spadix 5–12(16) flowered, 2–10 mm long at anthesis; blade punctate on upper surface, 2–7.5 cm long. .... *A. scandens* ssp. *pusillum* Sheffer

6b. Plants acaulescent or with short caudex and short internodes; plants never hanging (except *A. friedrichsthalii*); berries various colors; leaf blades usually much longer than 15 cm, occasionally slightly smaller.
  10a. Leaf blades oblong, strap-like; berries pale yellow-orange, broader in direction of axis than perpendicular to axis, sunken at apex.
    11a. Spathe to 5 mm wide, early deciduous; leaf blades mostly 1–4 cm wide; spadix sessile. .... *A. friedrichsthalii* Schott
    11b. Spathe 1–1.5 cm wide, usually persisting; leaf blades mostly 4–7.5 cm wide; spadix short-stipitate. .... *A. utleyi* Croat & Baker
  10b. Leaf blades not oblong; berries various.
    12a. Peduncle filiform, long and very fragile, the spadix often pendent; spathe tinged reddish-violet; berries peach-orange; all vegetative parts brittle; 0–800(1,400) m. .... *A. acutangulum* Engl.
    12b. Peduncle erect, elongate or short; spathe of various colors, usually green or purple; berries of various colors; vegetative parts not brittle; 0–1,700 m.
      13a. Peduncle 3-sided and alate; petiole triangular in cross-section; Osa Peninsula. .... *A. alatipedunculatum* Croat & Baker
      13b. Peduncle terete or nearly so (except *A. austinsmithii* sharply angulate); petiole not triangular in cross-section; primarily Atlantic watershed.
        14a. Leaf blades narrowly elliptic, the apex acuminate; spadix short (to 15 cm), on a stipe 1–6 mm long. .... *A. utleyi* Croat & Baker
        14b. Leaf blades lanceolate, oblanceolate, elliptic, or obovate; spadix very long or short (*A. lancifolium, A. paludosum*); spadix sessile or nearly so.
          15a. Leaf blades lanceolate to ovate-lanceolate or oblong-lanceolate, the apex long-acuminate; spadix grayish-white to violet-purple.
            16a. Peduncle terete; spadix grayish- or greenish-white, with four or five flowers visible in each spiral from any angle; berries violet-purple at maturity. .... *A. lancifolium* Schott
            16b. Peduncle 2- or 3-sided, sharply angular; spadix becoming violet-purple (may be green prior to anthesis), with no more than three flowers visible in each spiral from any angle; berries white, tinged with violet-purple at apex. .... *A. austinsmithii* Croat & Baker
          15b. Leaf blades lanceolate to obovate but never long-acuminate at apex; spadix color various.
            17a. Cataphylls thick, persistent, not dilacerating; petioles one sixth to one third as long as blades; blades almost oblong, coriaceous drying equally light green or yellow-green on both surfaces; fresh material with a conspicuous whitish midrib; berries orange; near sea level. .... *A. paludosum* Engl.
            17b. Cataphylls thin, soon weathering and deciduous; petioles various; blades mostly elliptic to oblanceolate or narrowly obovate, chartaceous or rarely coriaceous, drying usually brownish or grayish to blackened, usually paler on lower surface when fresh, the midrib not noticeably paler; berries orange to red; elevation various.
              18a. Leaves usually with moderately short petioles (one sixth to one third the length of the blade) and oblanceolate to narrowly obovate blades; peduncle and spadix usually stout; spadix usually very long, 4–10 mm diam. near base, gradually tapered to apex; berries pale red, flat at apex; 0–1,400 m. .... *A. ramonense* Engl. ex K. Krause
              18b. Leaves usually with longer petioles (one third to fully as long as blade) and elliptic or narrowly elliptic blades; peduncle slender or stout; spadix slender or stout, tapered or not, usually less than 5 mm diam. in *A. acutangulum* but sometimes to 10 mm diam. at base in *A. durandii*; berries orange to peach-orange.

19a. Blades short-acuminate, the acumen almost rounded or even emarginate at apex; cataphylls usually either deciduous or with few persisting as thin fibers, not forming a dense fibrous network. .... *A. durandii* Engl.
19b. Blades noticeably acuminate, the acumen obtuse at apex; cataphylls usually persisting as a dense fibrous network. .... *A. acutangulum* Engl.

KEY F

Leaves simple, not lobed; blades neither cordate nor subcordate at base, epunctate.

1a. Geniculum situated at least 7 cm below the base of the blade; plants terrestrial. ..... *A. oerstedianum* Schott
1b. Geniculum immediately subtending the leaf blade.
- 2a. Plants scandent, the stem elongate, with long internodes, the leaves dispersed throughout much of the length of the stem.
  - 3a. Spathe decurrent on the peduncle (0.5)1–1.5 cm; berries yellow to orange or white. .... *A. pittieri* Engl.
  - 3b. Spathe essentially not decurrent; berries green, yellow, orange or bright red to red-violet.
    - 4a. Stem with two or more successive, abbreviated internodes alternating with greatly elongated internodes, 8–33 cm long; leaves drying brownish-green or olive-green; berries bright red or purple-red; below 1,000 m. .... *A. interruptum* Sodiro
    - 4b. Stem with internodes nearly uniform length, decreasing slightly toward the apex of the stem; leaves drying dark brown to blackish or pale green; berries green, red or orange; usually above 1,200 m elevation, rarely below 1,000 m.
      - 5a. Petioles less than 3 cm long; peduncles less than 4 cm long, enclosed at base in an elongate leaf sheath. .... *A. tenerum* Engl.
      - 5b. Petioles more than 3 cm long, peduncles more than 5 cm long.
        - 6a. Blades drying black or blue-black, dark brown on the upper surface, medium brown on the lower surface; leaves fleshy when fresh; veins obscure; 1,500–2,600 m. .... *A. carnosum* Croat & Baker
        - 6b. Blades drying dark green to pale green above, pale yellow-green or occasionally brownish beneath; leaves thickly chartaceous; veins prominent below; 700–2,300 m.
          - 6′a. Spadix more than 7 cm long at anthesis, slender and narrowly tapered to apex; berries red, early emergent, oblong. .... *A. testaceum* Croat & Baker
          - 6′b. Spadix less than 5 cm long at anthesis, blunt and scarcely tapered to apex; berries yellow-green, not early emergent, more or less globose.
            - 7a. Petioles mostly more than 15 cm long; leaf base acute to rounded; stipe 1–5 mm long; leaves usually clustered at the ends of branches (internodes short) with the more elongate lower nodes usually leafless. .... *A. pallens* Schott
            - 7b. Petioles mostly less than 15 cm long; leaf base often truncate or subcordate; stipe 2–10 mm long; leaves evenly distributed along the branches and persistent, the apical internodes not usually shortened. .... *A. microspadix* Schott
- 2b. Plants not scandent, either appearing more or less acaulescent with the stem short or the stem elongate but with the internodes short, the existing leaves clustered near the end of the stem.
  - 8a. Petioles terete or subterete, never quadrangular, rectangular, or triangular, often narrowly or broadly sulcate on upper side with the margins sharp or blunt but merely rounded on lower side, never prominently ribbed on lower side.
    - 9a. Major lateral veins mostly free to the margins, sometimes weakly loop-connected in apical half of blade, never with a conspicuous, almost straight collective vein arising from near the base.
      - 10a. Peduncle usually shorter than petiole, never more than two times longer than petiole; spadix usually more or less oblong, usually short and thick, never long, linear-tapered; peduncle less than twice as long as spadix; berries red. *A. cubense* Engl.
      - 10b. Peduncle mostly two or more times longer than petiole; spadix usually elongate, cylindroid-tapered, never oblong (except *A. consobrinum*), if short then not thick; peduncle more than twice as long as spadix; berries red, white, cream, greenish, orange or yellow, not violet-purple.
        - 11a. Pistils acutely pointed at apex; berries white, cream, yellow, orange, sometimes white tipped with orange, yellow or reddish at apex only; species of the Atlantic slope.
          - 12a. Mature spadix cylindroid, not tapered, to ca. 9 cm long and 1.5 cm

(including pistils) diam. at anthesis, the pistils exserted well above the stamens and emerging weeks ahead of the stamens; berries white at base, reddish at apex; midrib rounded on lower leaf surface near the base of the blade. .... *A. consobrinum* Schott

12b. Mature spadix cylindroid-tapered, 12–15 cm long and ca. 8 mm diam. at base at anthesis, the pistils not apparent before anthesis, obscured by the stamens when stamens are exserted; berries white, cream, yellowish, or orange, usually a solid color throughout; midrib usually more or less trapezoidal with two sharp ribs on the lower leaf surface near the base of the blade. .... *A. fatoense* K. Krause

11b. Pistils not emerging early, rounded at apex; berries greenish-white or red, usually blunt at apex; roots 3 mm or more thick, free-ending or not but not all uniformly turned upward, not conspicuously acute at apex.

13a. Spathe ovate, pale green, erect, and enshrining the spadix; spadix pale green, moderately stubby, usually less than 6.5 cm long; plants usually terrestrial or on soil deposits on rocks; blades usually elliptic; roots mostly 1 cm diam. when fresh; eastern Guatemala and western El Salvador on the Pacific slope. .... *A. salvadorense* Croat

13b. Spathe lanceolate (except *A. halmoorei*), usually green to violet-purple, reflexed or spreading; spadix green to pale lavender or purplish, usually rather slender and long-tapered, usually more than 6.5 cm long; plants usually epiphytic or epipetric (except *A. nizandense*); blades usually oblanceolate-elliptic to oblanceolate (except sometimes elliptic on *A. nizandense*); roots mostly less than 6 mm diam. when fresh; Mexico to Colombia.

14a. Leaf blades obovate-elliptic, 1.3–2.5 times longer than petioles, less than 3 times longer than broad; Mexico in southern Oaxaca and Guerrero. .... *A. nizandense* Matuda

14b. Leaf blades generally oblanceolate or oblanceolate-elliptic, 3 or more times longer than petioles; usually 3 or more times longer than broad.

15a. Spathe ovate to broadly ovate; berries pale greenish-yellow; western Mexico in Nayarit, Jalisco, Colima, and Michoacán. .... *A. halmoorei* Croat

15b. Spathe lanceolate to linear-lanceolate; berries bright red; Mexico from Guerrero to Chiapas and Veracruz and to Colombia.

16a. Cataphylls cucullate (hooded), fist-shaped before opening; inflorescence frequently pendent at anthesis; spadix usually long-tapered, pale lavender, weakly glaucous; spathe long and narrowly tapered to apex, spreading, thin, almost as long as the spadix; Pacific slope except from Nicaragua to Panama. .... *A. salviniae* Hemsl.

16b. Cataphylls lanceolate; inflorescence usually erect; spadix short-tapered, green to violet-purple, not glaucous; spathe moderately short, reflexed, coriaceous, usually much shorter than spadix.

17a. Plants occurring on rocky, dry slopes; Pacific slope of Mexico in Guerrero and southern Oaxaca. .... *A. schlechtendalii* ssp. *jimenezii* (Matuda) Croat

17b. Plants occurring as epiphytes or on rocks in usually moist areas; Atlantic slope, principally from Veracruz to Honduras. .... *A. schlechtendalii* Kunth ssp. *schlechtendalii*

9b. Major lateral veins mostly joining into a straight or conspicuously loop-connected collective vein, this arising usually in the lower half of the blade; plants with or without the rosulate habit.

18a. Spadix with no more than two to five flowers exposed across its diameter in any spiral from any angle of view.

19a. Leaf blades broadest above the middle, tapered to a long cuneate base; spathe red-violet; spadix purple-brown; berries red; roots usually white. .... *A. gracile* (Rudge) Lindl.

19b. Leaf blades broadest at or below the middle, acute to rounded at base; spathe

green; spadix green, yellow or orange, sometimes tinged purple; berry color various.

20a. Spathe decurrent onto peduncle (0.5)1–1.5 cm; pistils early emergent many times longer than stamens at anthesis; berries yellow or orange. .... *A. pittieri* Engl. ssp. *pittieri*

20b. Spathe not long-decurrent onto peduncle; pistils scarcely longer than stamens at anthesis; berries green or red (not known in *A. pittieri* var. *fogdenii* but probably orange).

21a. Spathe to 7 cm long; spadix 4–12 cm long; berries red. .... *A. testaceum* Croat & Baker

21b. Spathe less than 3.5 cm long; spadix less than 4.5 cm long; berries greenish (*A. pallens*) or probably orange (*A. pittieri* var. *fogdenii*).

22a. Leaf blades less than 10 cm long, thick, veins shallowly etched above, obscure below; primary lateral veins three to four per side. .... *A. pittieri* var. *fogdenii* Croat

22b. Leaf blades more than 15 cm long, moderately thin, tertiary veins prominulous below (dry), primary lateral veins five to nine per side. .... *A. pallens* Schott

18b. Spadix with more than five flowers exposed across its diameter in each spiral from any angle of view.

23a. Petioles mostly less than 10 cm long; blades usually six or more times longer than petioles.

24a. Collective vein arising from one of the primary lateral veins, well above the base; berries white at base, reddish or purplish at apex; pistils early long-exserted, much longer than the stamens. .... *A. consobrinum* Schott

24b. Collective vein arising from the base of the blade; berries red (not seen for *A. machetioides*); pistils not long-exserted, held at about the same level as stamens.

25a. Spadix stubby, creamy-white; spathe lanceolate-ovate, clasping at the base; cataphylls thick, persisting intact; Costa Rica on the Pacific slope. .... *A. eximium* Engl.

25b. Spadix slender and long-tapered, greenish; spathe lanceolate, acute or obtuse at the base; cataphylls thin, weathering into fibers; Mexico in Oaxaca. .... *A. machetioides* Matuda

23b. Petioles usually 11 cm or longer; blades no more than four times longer than petioles.

26a. Species of Mexico and Middle America, ranging as far south as northern Honduras; petioles broadly sulcate adaxially, the margins obtuse or acute.

27a. Leaf blades lacking any obvious basal veins, the lowermost primary lateral veins more or less equal or less prominent than those higher up on the blade.

28a. Tertiary and higher order veins conspicuously elevated (at least when dry). .... *A. retiferum* Standl. & Steyerm.

28b. Tertiary and higher order veins obscure, much less prominent than the primary lateral veins. .... *A. parvispathum* Hemsl.

27b. Leaf blades with usually well developed basal veins which are more prominent than the primary lateral veins or at least unite to form a posterior rib.

29a. Collective vein arising from one of the lowermost basal veins; primary lateral veins numerous or apparently so, scarcely more prominent than the interprimary or tertiary veins; blade often conspicuously broadened at the base. .... *A. seleri* Engl.

29b. Collective vein arising from the uppermost basal vein or even from one of the primary lateral veins; primary lateral veins usually conspicuously more prominent than the interprimary or tertiary veins; blade usually not conspicuously broadened at the base (sometimes so in *A. nakamurae*).

30a. Blades broadest near or even above the middle, six or more times longer than broad; southwestern Chiapas. .... *A. nakamurae* Matuda

30b. Blades broadest near the base, usually ca. three times longer than broad.

31a. Major veins of lower blade surface reddish (at least on younger leaves); northern Oaxaca. .... *A. subovatum* Matuda

31b. Major veins of lower blade surface green; Guatemala to Honduras. .... *A. subcordatum* Schott

26b. Species of Costa Rica and Panama or possibly as far north as Nicaragua; petioles sulcate or not.

32a. Major lateral veins obscure (prominulous when dry but scarcely more prominent than the tertiary venation); the midrib reddish in lower half of blade (less noticeable after drying); cataphylls not dilacerating, soon deciduous. .... *A. burgeri* Croat & Baker

32b. Major lateral veins prominent, much more conspicuous than the tertiary veins; midrib not reddish; cataphylls usually dilacerating at least at base, usually persisting for a considerable time.

33a. Cataphylls less than 15 cm long and less than 1 cm wide at the middle, weathering into mostly longitudinal fibers; stem mostly ca. 1 cm diam., elongate, with many white to tan roots among the existing leaves; inflorescences usually erect at anthesis, arching in fruit; spadix usually less than 6 mm diam. at base, berries pale green. .... *A. angustispadix* Croat & Baker

33b. Cataphylls more than 15 cm long or more than 1.5 cm wide at the middle, often weathering into a net-like structure (with coarse longitudinal fibers underlain by finer, diagonally directed fibers), or remaining intact near apex; stem mostly 2 cm diam. or more, usually lacking white to tan roots among the existing leaves; inflorescences usually spreading to pendent at anthesis, pendent in fruit (except *A. cuspidatum*); spadix mostly more than 7 mm diam. at base (except *A. protensum* and *A. cuspidatum*); berries not pale green.

34a. Leaf blades ovate to oblong-ovate, mostly more than 20 cm wide, truncate to subcordate at base, the basal veins united into a short trunk vein. .... *A. cuspidatum* Mast.

34b. Leaf blades oblong to oblong-elliptic, mostly less than 20 cm wide, acute to attenuate or subrounded at base, lacking a posterior rib.

35a. Spathe and spadix less than 8.5 cm long; spathe ovate, cordate at base, ca. half as wide as long. .... *A. brenesii* Croat & Baker

35b. Spathe and spadix more than 10 cm long; spathe lanceolate to linear, not cordate, much more than twice as long as wide.

36a. Leaves much paler and whitish beneath; spadix yellow-green; rosulate plant with erect-spreading leaves; blades to 54 cm long. .... *A. michelii* Guillaumin

36b. Leaves more or less concolorous; spadix purplish or purplish tinged; plant and/or leaves usually pendent; blades often more than 60 cm long.

37a. Spadix 30–75 times longer than wide, to ca. 60 cm long, the fruiting spadix more than 30 cm long; flowers more than 1.8 mm wide (dry) at apex; plants occurring below 600 m. .... *A. prolatum* Croat & Baker

37b. Spadix less than 20 times longer than wide at anthesis, to 20 cm long, the fruiting spadix usually less than 25 cm long; apex of flowers less than 1.5 mm wide; plants occurring above 900 m. .... *A. protensum* Schott

8b. Petioles quadrangular, rectangular, decidedly triangular or prominently 1- or more ribbed on lower (abaxial) side.

38a. Major lateral veins mostly free to the margin, sometimes loop-connected in apical half of blade, never with a continuous, almost straight collective vein arising from near the base; plants rosulate epiphytes with usually short stems and massive root clusters among the petioles; berries pale orange, yellow or red.

39a. Stem usually 1–1.5 cm diam., comparatively elongate, at least the lower internodes not completely obscured by the roots; inflorescences usually arched-spreading; infructescence pendent, the spadix greenish to white or pale reddish to pale purple.

40a. Leaf blades thickly chartaceous; berries cream to pale orange or yellow; roots many, compact, more or less contiguous, tapering, slender, ascending; petioles mostly less than 10 cm long. .... *A. fatoense* K. Krause

40b. Leaf blades subcoriaceous; berries red; roots moderately dense, thick, blunt, not ascending; petioles mostly more than 10 cm long. .... *A. upalaense* Croat & Baker

39b. Stem usually more than 2.5 cm diam. (at least on mature individuals), the internodes mostly completely obscured by the roots, the roots moderately stout, usually more than 3 mm diam., not all elongate tapered and regularly directed upwards; inflorescence erect or spreading; infructescence erect or pendent; spadix dark violet-purple or green or green tinged purplish.

41a. Species occurring from Mexico to El Salvador, frequently on rocks; berries red or pale greenish-yellow or greenish-white.

42a. Leaf blades obovate-elliptic, less than three times longer than broad, 1.3–2.5 times longer than petioles; southern Oaxaca and Guerrero. .... *A. nizandense* Matuda

42b. Leaf blades generally oblanceolate or oblanceolate-elliptic usually three or more times longer than broad; blades three or more times longer than petioles.

43a. Spathe green, ovate.

44a. Spathe erect and enshrining the spadix; berries orange-red; eastern Guatemala and western El Salvador on the Pacific slope. .... *A. salvadorense* Croat

44b. Spathe reflexed; berries pale greenish-yellow; petiole obtusely 3-sided; western Mexico in Nayarit, Jalisco, Colima, and Michoacán. .... *A. halmoorei* Croat

43b. Spathe green or usually violet-purple, lanceolate.

45a. Plants from the Pacific slope in Guerrero and Oaxaca; dry rocky slopes. .... *A. schlechtendalii* ssp. *jimenezii* (Matuda) Croat

45b. Plants principally from the Atlantic slope; epiphytes or on rocks in generally moist areas. .... *A. schlechtendalii* Kunth ssp. *schlechtendalii*

41b. Species of Costa Rica and Panama to as far north as Nicaragua.

46a. Peduncles usually shorter than petioles, rarely to 1.5 times longer than petioles; petioles usually sharply quadrangular, flat or 3-ribbed on lower side (abaxial), the sides unribbed; spathe purplish; spadix often short, 5–22 cm long; pistils emerging early; berries red, acute at apex. .... *A. purpureospathum* Croat

46b. Peduncles usually 1.5–3 times longer than petioles; petioles subquadrangular, lacking abaxial ribs; spathe 16–17 cm long, green; spadix 15–23 cm long; pistils not emerging early; berries orange, flattened at apex. .... *A. validifolium* K. Krause

38b. Major lateral veins mostly joining into a straight or conspicuously loop-connected collective vein, this usually arising in the lower half of the blade; plants with or without the rosulate habit; berries green, red, violet-purple or orange.

47a. Spadix cylindroid to clavate, as broad as or broader toward apex as at middle; spathe broadly ovate or narrowly ovate; berries greenish to white or red.

48a. Spadix usually clavate or subclavate; cataphylls soon weathering to longitudinal, persistent, pale fibers; spathe cucullate, ovate; berries greenish; plants of the Atlantic slope from 0–650 m.

49a. Blades with 20–30 pairs of primary lateral veins, these prominently sunken; spathe lanceolate to broadly lanceolate, about twice as long as the spadix; petiole commonly triangular, 3–5-ribbed. .... *A. spathiphyllum* N. E. Brown

49b. Blades with (5)10–15 pairs of primary lateral veins, these weakly sunken; spathe ovate, about as long as the spadix; petiole commonly quadrangular. .... *A. cuneatissimum* (Engl.) Croat

48b. Spadix usually cylindroid; spathe more or less planar, lanceolate-ovate; cata-

phylls persistent, turning brown but not dilacerating; berries red; plants of the Pacific slope in tropical wet forest from 0–50 m. .... *A. eximium* Engl.

47b. Spadix usually conspicuously tapered toward the apex; spathe narrowly ovate to lanceolate or oblong-lanceolate; berries greenish, violet-purple, orange or red.

50a. Petioles triangular, acutely 1-ribbed on lower (abaxial) side; blades markedly bicolorous, the lower surface creamy-green, drying black to olive-brown, lower surface with the major veins conspicuously darker than the surface, scarcely or not at all raised, the tertiary veins obscure; berries bright violet-purple, acute at apex. .... *A. michelii* Guillaumin

50b. Petioles quadrangular, usually 3-ribbed on lower (abaxial) side; blades not markedly bicolorous but usually somewhat paler beneath, usually drying green, lower surface with the major lateral veins usually somewhat lighter than the lower surface, usually conspicuously raised (scarcely raised in *A. upalaense* but with the tertiary veins prominently visible); berries greenish, orange or red.

51a. Plants terrestrial; blades attenuate at base (broadly concave between lower third of blade and geniculum); berries greenish-yellow. .... *A. acutifolium* Engl.

51b. Plants epiphytic; blades acute to truncate or rounded at base; berries orange or red.

52a. Major lateral veins scarcely raised; blades acute at base, the tertiary veins clearly visible but not at all raised (except after drying), about as prominent as the collective vein and the distal parts of the major lateral veins; cataphylls turning brown, remaining intact, not dilacerating; berries bright red. .... *A. upalaense* Croat & Baker

52b. Major lateral veins prominently raised; blades acute to truncate or subcordate at base, tertiary veins weakly raised (even on fresh material), much less conspicuous than the collective vein and distal parts of the major lateral veins; cataphylls usually tan, dilacerating at least at base; berries orange (presumed orange for *A. spectabile*).

53a. Peduncles usually greatly exceeding petioles when fully mature; blades usually less than 16 cm wide; spadix usually less than 20 cm long at anthesis; stamens held just above tepals, the filaments usually not visible; anthers ca. 0.5 mm long. .... *A. seibertii* Croat & Baker

53b. Peduncles usually shorter than petioles; blades usually more than 20 cm wide; spadix usually more than 20 cm long at anthesis; stamens prominently exserted above the tepals, the filaments exposed; anthers ca. 0.9 mm long. .... *A. spectabile* Schott

Anthurium Schott, Wiener Z. Kunst 3: 828. 1829.

Herbs, usually epiphytic, rarely terrestrial (more commonly so in cloud forests where they grow on deposits of debris), the growth habit monophyllous or polyphyllous sympodial; stems nontuberous, the internodes short to elongate (plants then often scandent), the leaf scars often very conspicuous; cataphylls usually ± lanceolate (rarely cucullate), usually green, soon drying and then variously colored, with a medial rib beginning somewhere above the middle, usually extending to the apex (the rib sometimes ending in a subapical apiculum), deciduous or persisting, often weathering into coarse or fine fibers. LEAVES commonly clustered at or near the apex of the stem; petioles usually firm, stiff or flexible, sheathed near the base, geniculate at apex, the cross-sectional shape variable, frequently subterete and narrowly sulcate, sometimes with few to several ribs, the sulcus various, with the margins sharp or blunt; blades usually coriaceous to subcoriaceous, very variable in form, simple and usually ovate, elliptic or lanceolate or digitately lobed, net-veined, the primary lateral veins and/or basal veins often forming a collective vein, the basal veins often united at base forming a posterior rib on leaves with posterior lobes. INFLORESCENCE one per node (often aborting), held below or above the leaves; peduncle terete or angular, usually elongate; spathe usually flat, usually not convolute at base, persistent, usually free well before anthesis of the flowers, usually

spreading or strongly reflexed from the spadix, sometimes erect, sometimes hooding spadix, often colored, usually ± lanceolate, often ± elliptic or ovate, usually inserted on the peduncle at an oblique angle and often also decurrent; spadix uniform, usually cylindroid-tapered, sometimes cylindroid, clavate, or subglobose, sessile or stipitate, many flowered, variously colored, elongated in fruit, usually flowering from the base upward in a slow or rapid progression, sometimes beginning from the middle and developing rapidly throughout the spadix; flowers perfect, usually protogynous, closely aggregated in spirals, truncate and usually rhombic in outline at apex, sometimes the outline sub-4-lobed (i.e., margins of apex) straight or gradually or jaggedly sigmoid; principal spirals with flowers aligned, their lateral margins forming a straight row; alternate spirals (opposite direction) with flowers aligned, their lateral margins not forming a straight row; tepals flattened throughout most of their length, broader and truncate at apex (somewhat accrescent in fruit), usually triangular, the inner margin usually rounded, held above the ovary, sometimes turned up against the emerging ovary, sometimes overlapping before anthesis, the surface glossy to matte, sometimes with nectar droplets, especially while anthers are emerging; the space between the tepals (exposed part of pistil) usually square or rectangular, sometimes elliptic; pistil simple, 2-celled, included or exserted at anthesis, green or variously colored, usually rounded at apex, rarely acute to truncate; style usually absent; stigma usually a slitlike depression lined with papillae, usually linear to elliptic, sometimes inverted and brushlike with rather elongate papillae, usually forming stigmatic droplets at anthesis; ovules usually 1 or 2 per cell, rarely 3 or more; stamens 4, usually weakly exserted, sometimes well exserted, less frequently included with only the pollen emerging from beneath the tepals, usually the lateral pair of stamens emerging first one at a time, followed by the anterior and posterior ones, the filaments flattened, somewhat rounded abaxially when exserted, usually narrowed to the connective, usually included and not visible, sometimes exserted, then frequently withdrawing after anthesis to position the anther at the level of the tepal, sometimes withdrawing the anther below the tepals; anthers usually broader than long, the thecae broadly ovate to oblong-ovate, opening by a longitudinal slit. INFRUCTESCENCE usually pendent, rarely erect; berries ovoid, oblong-ovoid, oblong, or obovoid, less frequently depressed-globose, usually acute to rounded or truncate at apex, sometimes with a depression at apex, exserted and dangling on 4 threads at maturity, succulent and juicy, variously colored, 2-celled, usually 2-seeded, sometimes 4- or more seeded.

DISCUSSION OF MORPHOLOGICAL CHARACTERS PRESENTED OR OMITTED FROM SPECIES DESCRIPTIONS

In order to provide detailed descriptions of the species presented here and at the same time to provide relatively short descriptions, a number of assumed character states will be listed for the genus. While these might be apparent upon rereading the generic description, this list should more readily elucidate assumed characters.

Stems: Usually assumed short unless a specific length is given.

Internodes: As above.

Cataphylls: Assumed 1-ribbed.

Petiole: Color mentioned only if other than green.

Geniculum: Shape and color given only if different from petiole.

Leaf Color: Mentioned only if other than green or if lower surface is substantially paler than upper surface.

Leaf Texture: Usually mentioned only if other than semiglossy.

Venation: Basal veins and midrib assumed raised unless otherwise indicated.

Inflorescence: All colors given are assumed to be at anthesis unless otherwise stated; spadix assumed to be cylindroid-tapered unless otherwise stated.

Flower size: "Length" is actually the width of the apical, thickened part of the flower in the direction of the axis; "width" is the width of the apical part of the flower, perpendicular to the axis (only the visible portion is measured); "sides of the flower" refers to the line formed by the 4 outer margins of the apex of the flower (see Croat & Bunting, 1979).

Filaments: Length and width is the measurement of the area exposed.

See Croat and Bunting (1979) and Croat (1980) for details of flowering behavior to understand the necessarily abbreviated discussion of staminal behavior in *Anthurium*. The discussion of flowering behavior under the section of this paper entitled "Taxonomic Characters" (Inflorescences) gives information essential to understanding the descriptions of this behavior in the following treatment of species.

Anthurium acutangulum Engl., Bot. Jahrb. Syst. 25: 371. 1898. TYPE: Costa Rica. San José: near San José, 1,200 m., *Tonduz 10360* (B, hololectotype; CR, isolectotype; designated Croat & Baker, 1979).

Anthurium porschianum K. Krause, Ann. Naturhist. Mus. Wien 46: 231. 1932. TYPE: Costa Rica. Limón Prov.: La Castilla-Los Negritos, 12 km from the mouth of the Río Reventazon, 20 m, *Cufondontis 611* (W, holotype; B, isotype).

Epiphyte or rarely terrestrial; roots numerous; cataphylls subcoriaceous, 2.5–5(11) cm long, acuminate (the acumen apiculate), drying tan to light brown, persisting as linear fibers. LEAVES erect to spreading; petioles narrowly sulcate, rounded to sometimes 1-ribbed abaxially, 3–22 cm long, 4–7 mm diam.; geniculum 1–1.5 cm long; blades elliptic to narrowly obovate, subcoriaceous, short-acuminate at apex, acute to obtuse at base, 15–34 cm long, 5–14 cm wide, broadest at middle or slightly above, both surfaces semiglossy, the lower surface punctate; midrib convexly raised above and below; primary lateral veins 8–10 per side, departing midrib at 55°–60° angle, ± straight to collective vein, loop-connected from base; collective vein rising from base, sunken on upper surface, 3–8 mm from margin. INFLORESCENCE spreading to pendent, equal to or longer than leaves; peduncle 12–61 cm long, 4–4.5 mm diam., terete or strongly ribbed abaxially, sometimes 3-ribbed adaxially, rarely 4–6 ribbed, the ribs irregularly spaced, tinged with red-violet near base, much longer than petioles; spathe green, tinged with red-violet (B & K Yellow-green 8/10), oblanceolate, 7–11.5 cm long, 1.2–1.5 cm wide, broadest at base, inserted at 40° angle on peduncle, sometimes slightly twisted; stipe 6–7 mm long in front, 2–3 mm long in back; spadix yellow-green (B & K Yellow-green 6/7.5), 8.5–21 cm long, 4–6 mm diam. at base, 3–4 mm diam. at apex; flowers rhombic, 4.2–6 mm long, 2.5–3.5 mm wide, the sides ± straight; ca. 5 flowers visible in the principal spiral and ca. 4–6 flowers visible in the alternate spiral; tepals glossy, weakly punctate, papillate; lateral tepals 3–3.3 mm wide, the inner margins straight and flat; pistils emergent, green; stigma brushlike with droplets, dry and brown as stamens emerge; stamens emerging rapidly from base or middle, the first lateral stamens emerging at apex as third and fourth emerge at base, exserted on transparent filaments, 0.3–0.5 mm long, 0.7–1 mm wide, retracting and holding anthers at sides of pistil, not contiguous; anthers creamy white, 0.5 mm long, 0.7–0.8 mm wide; thecae ellipsoid, divaricate; pollen white, abundant. INFRUCTESCENCE pendent; berries pale orange, ± obovoid, ca. 5 mm long. Figs. 2 and 3.

The species is known from Honduras (la Mosquitia) to Panama from sea level to 1,400 m. It is found only on the Atlantic slope in Honduras and Nicaragua, but on both slopes in Costa Rica and Panama. In Panama it occurs on the Pacific slope near the Continental Divide. *Anthurium acutangulum* is known from wetter parts of tropical moist, premontane wet, and tropical wet forest.

Anthurium acutangulum is recognized by its long-petiolate, more or less elliptic, glandular-punctate leaves, which are abruptly acuminate at apex; its slender, pendulous inflorescence; its peduncle and spathe that are usually tinged red-violet, and its pale orange berries.

This species is a typical member of section *Porphyrochitonium* despite its erroneous placement in section *Leptanthurium* by Engler (1905). The species is most easily confused with smaller specimens of *A. ramonense* but that species has a much stouter peduncle and the inflorescence is either held semierect or, if it is pendent, it is held stiffly downward and outward, not hanging loosely as in the case of *A. acutangulum*. In addition, the pistils of *A. ramonense* are not at all raised, the exposed portion being markedly squared and violet-purple. In *A. acutangulum* the pistils are green, appear somewhat rounded, and are promptly raised well above the tepals, giving the spadix a weakly knobby appearance.

COSTA RICA. ALAJUELA: between Cañas and Upala, N of Bijagua, *Croat 36481* (MO); Santa María National Park, *Liesner 5130* (MO); NW of Zarcero, *Croat 43581* (MO). CARTAGO: valley of Río Tuis, *Tonduz 8217* (BR). GUANACASTE: Le Tejonia, *Standley & Valerio 46028* (US). LIMÓN: S of Siguirres, *Croat 43340* (MO). SAN JOSÉ: between División and Palmital, *Pittier 3868* (BR). HONDURAS. GRACIAS A DIOS: near Río Plátano, *Clewell & Cruz 4121* (MO).

FIGURES 2–5. 2. *Anthurium acutangulum* Engl., *Croat 43340*.—3. *Anthurium acutangulum* Engl., *Croat 6740*.—4. *Anthurium acutifolium* Engl., *Pittier 6539* (Lectotype).—5. *Anthurium alatipedunculatum* Croat & Baker, *Utley 1030* (Type).

NICARAGUA. RÍO SAN JUAN: near Caño Chontaleño, NE of El Castillo, *Neill 3422* (MO). ZELAYA: Caño Zamora, *Stevens 8834* (MO); *Stevens et al. 8862* (MO); Caño Majagua, *Stevens 6976* (MO); S slope of Cerro El Inocente, *Stevens 6804* (MO); SE of Cerro San Isidro, Río Kama, *Proctor et al. 26993* (LL, NY); Cerro Saslaya, W of Siuna, *Neill 1875* (MO); road to Colonia Agricola Yolaina & Colonia La Esperanza, *Stevens 6309A*; *Vincelli 167* (MO); near El Recreo, *Neill & Atwood AN 226* (MO); beyond Kururia, on road to San Jerónimo, *Stevens 7557* (MO); 8 km N of La Cruz, *Neill 4347* (MO); new road to Mina Nueva America, N of El Empalme, *Stevens 8335, 8412* (MO); between Rosita and Puerto, SW of Río Kukalaya, *Stevens 8506, 8645* (MO); W of Rosita Empalme, *Neill 4111* (MO); Caño at Salto La Oropéndola, *Stevens 8947* (MO); along road from Siuna to Matagalpa, *Stevens 7523* (MO); near Tala Has and Puente Mango, *Stevens 7608* (MO); N of Limbaika, near Río Prinzapolka, *Stevens 8253* (MO).

Anthurium acutifolium Engl., Bot. Jahrb. Syst. 25: 365. 1898. TYPE: Costa Rica. Puntarenas: along the Río Hakum, Buenos Aires (SE of San Isidro del General), elev. 250 m, *Pittier 6539* (B, hololectotype; BR, CR, isolectotypes; designated Croat & Baker, 1979).

Anthurium scopulicola Standl. & L. O. Wms., Ceiba 3: 105. 1952. TYPE: Costa Rica. Puntarenas: vicinity of Palmar Norte, elev. near sea level, *P. H. Allen 5788* (EAP, holotype; F, isotype).

Terrestrial or rarely epiphytic; roots numerous, thick, velutinous; cataphylls persisting as fibrous network, subcoriaceous, 6–10 cm long, acuminate at apex (the acumen apiculate), drying dark tan (B & K Yellow 5/5). LEAVES erect to spreading; petioles (2)6–22 cm long, (3)6–9 mm diam., flattened to broadly sulcate adaxially, sharply 3-ribbed abaxially; blades epunctate, oblanceolate to broadly oblanceolate, gradually acuminate at apex, long attenuate at base, (11)25–62 cm long, (3.5)5.5–27 cm wide, broadest at middle; midrib raised above and below, paler than surface, sometimes yellow; primary lateral veins 8–12 per side, departing the midrib at 40°–45° angle; collective vein arising from the third to fifth primary lateral vein, 3–5 mm from the margin. INFLORESCENCE erect, usually shorter than leaves; peduncle 24–53 cm long, 3–5 mm diam., much longer than petioles; spathe green, linear-lanceolate, 5–12 cm long, 0.7–1.1 cm wide; spadix sessile, green to white, sometimes tinged with red-violet, 7–16 cm long, 6–8 mm diam. at base, 3–4 mm diam. at apex; flowers square to rhombic, ca. 2 mm in both directions, the sides ± straight; 5–6 flowers visible in the principal spiral, 5–7 flowers visible in the alternate spiral; lateral tepals 0.5 mm wide, the inner margins turned up. INFRUCTESCENCE with greenish-yellow, obovoid berries often not developing in apical one quarter to one half of spadix. Fig. 4.

The species is known from Costa Rica and Panama in tropical moist, premontane wet, and tropical wet forest life zones at elevations of sea level to 900 m. The species has been collected once on the Atlantic slope and lowlands in San José and Puntarenas Provinces of Costa Rica, including the Osa Peninsula. It has been collected in Panama only on the Burica Peninsula in Chiriquí Province.

Anthurium acutifolium is a member of section *Pachyneurium* and is distinguished by being a terrestrial plant (rarely epiphytic) with thin, oblanceolate to broadly oblanceolate leaf blades that are attenuate at the base. The petiole is broadly sulcate to flattened on the upper side and sharply 3-ribbed on the lower side. The syntype *Pittier 4099* at MO is unusually small for the species but appears to differ in no other way.

Anthurium acutifolium is similar vegetatively to *A. consobrinum* but that species is an epiphyte (apparently restricted to the Atlantic slope) with early emergent, narrowly acute pistils, an oblong spadix, and a petiole that is rounded on the lower side. Pistils of *A. acutifolium* are not early emergent and are rounded at the apex.

COSTA RICA. ALAJUELA: El Rodeo, *Hunnewell 16560* (GH). GUANACASTE: Cabecera, *Pittier 11129* (BR, US). PUNTARENAS: Boruca, *Pittier 4656* (BR); Buenos Aires, *Pittier 6539* (BR); Burica Peninsula, S of Puerto Armuelles, *Croat 22127* (MO); Quebrada Palito, *Croat 22614* (MO); Osa Peninsula, at Sirena, *Liesner 2921* (MO); above Palmar Norte, *Croat 32926* (MO). SAN JOSÉ: Puriscal, Cerro Turrubares, *Jiménez 628* (US); between Río Cañas and Buenos Aires, *Pittier 3862* (BR); S of bridge over Río del General, *Harmon & Fuentes 6210* (UMO); basin of El General, *Skutch 4749* (MO); Pacaca, *Pittier 4099* (BR); near Santa Ana, *Burger & Liesner 7171* (MO); NW of Santa Ana, *Taylor 17387* (NY, US).

Anthurium alatipedunculatum Croat & Baker, Brenesia 16 (Supl. 1): 19. 1979. TYPE: Costa Rica. Puntarenas: Rincón de Osa, region SW of air strip, 20–60 m elevation, 20 July 1974, *Utley & Utley 1030* (F, holotype; MO, isotype).

Epiphyte; stems 1–1.5 cm diam.; roots few, descending, 2–3 mm diam.; cataphylls moderately thin, 2–3 cm long, acuminate at apex, drying brown, weathering into fibers, subpersistent.

LEAVES erect; petioles 4–26 cm long, 5–6 mm wide, triangular, sulcate, drying with a narrow, almost membranous wing; geniculum 0.5–1.2 cm long; blades lanceolate-elliptic, acuminate at apex, obtuse to rounded at base, 15–23.5 cm long, 6–10 cm wide, broadest below the middle, obscurely and sparsely punctate above, densely punctate below, the punctations reddish-brown, the margin drying conspicuously undulate; lower surface paler than upper; primary lateral veins 10–20 per side, departing midrib at 55° angle, almost straight to collective vein; interprimary veins numerous; collective vein arising from the base, 3–8 mm from margin. INFLORESCENCE shorter than leaves; peduncle 12–19 cm long, ca. 3 mm wide, winged, 0.5 to 5 times longer than petioles; spathe green suffused with purple-red at margin, lanceolate-linear, 3–4.5 cm long, 6–8 mm wide, broadest at base, short-acuminate at apex (the acumen apiculate), inserted at ca. 30° angle on peduncle; spadix sessile, green, 10–12 cm long, 3–5 mm diam. at base, 2–3 mm diam. at apex; flowers rhombic, 2.3–2.8 mm long (dry), 1.8–2.3 mm wide (dry), the sides ± straight to weakly sigmoid; 4–5 flowers visible in the principal spiral, 3–5 flowers visible in the alternate spiral; tepals drying matte, the lateral tepals ca. 2 mm wide (dry), the inner margins broadly rounded; stamens emerging just above the tepals, the anthers ca. 0.4 mm long, 0.9 mm wide (dry); thecae strongly divaricate. INFRUCTESCENCE not seen. Fig. 5.

The species is known only from the Osa Peninsula in tropical wet forest at less than 100 m elevation.

Anthurium alatipedunculatum is most closely allied to *A. acutangulum* but differs in having a winged, angulate peduncle and a triangular petiole which is sharply sulcate adaxially. The species is a member of section *Porphyrochitonium.*

COSTA RICA. PUNTARENAS: Rincón de Osa, region SW of air strip, *Utley & Utley 1030* (F, holotype; MO, isotype).

Anthurium andicola Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1: 22. 1849. TYPE: Mexico. Veracruz: Santa María Alpatlahua (NE of Coscomatepec) on slopes of Volcán Orizaba, 2,500 m. *Liebmann* (K, hololectotype here designated).

Anthurium cucullatum C. Koch, Index Sem. Hort. Berol. App. 6. 1853. *Anthurium andicola* var. *cucullatum* (C. Koch) Engl., Monogr. Phan. 2: 169, N. 97. 1879. TYPE: Origin unknown (cultivated).

Anthurium macdougallii Matuda, Anales Inst. Biol. Univ. Nac. México 25: 216, fig. 55, 1954. TYPE: Mexico. Oaxaca: Tenango, 1,300–1,700 m, *MacDougall s.n.* (MEXU, holotype).

Anthurium oaxacamonticolum Matuda, Anales Inst. Biol. Univ. Nac. México 27: 344. 1957. TYPE: Mexico. Oaxaca: vic. La Gloria, near the Oaxaca-Chiapas border, *MacDougall s.n.* March 5, 1953 (MEXU, holotype).

Anthurium campii A. D. Hawkes (not published). TYPE: Mexico. Oaxaca: near Ayutla, *Camp 2362* (NY).

Anthurium chochotlensis Matuda, Cact. Suc. Mex. 20: 11. 1975. TYPE: Mexico. Oaxaca: Chochotla (probably Santa María Chilchotla at 18°14′N; 96°49′W), Huatla de Jiménez, *Matuda 38620* (MEXU, holotype).

Epiphytic or on rocks, sometimes in soil on rocky cliffs; stems less than 20 cm long; leaf scars ca. 1.7 cm wide; roots thick, descending; cataphylls subcoriaceous, 2–4.5 cm long, tinged red at margins and apex, the apex round, minutely apiculate, drying medium brown (B & K Yellow 5/5), weathering to fibrous network at base. LEAVES with petioles erect to spreading, 18–47 cm long, 4–8 mm diam., sharply sulcate, weakly glaucous; geniculum 1.5–2 cm long, faintly tinged red; blades broadly ovate-deltoid, thick, narrowly acuminate at apex (rarely rounded), usually prominently lobed at base (rarely merely obtuse), 20–37.5 cm long, 13–27 cm wide, broadest at point of petiole attachment; anterior lobe 19–29 cm long, the margins broadly rounded; posterior lobes 7.5–13 cm long; sinus arcuate with decurrent petiole to parabolic to sometimes hippocrepiform; both surfaces matte to semiglossy, the lower surface weakly glaucous; midrib convexly raised above, diminished and flat at apex, more acutely raised below; basal veins 3–6 pairs, the first free to base, those remaining coalesced 1–3 cm, posterior rib naked, weakly curved, the outer margin scarcely turned up; primary lateral veins 3–5 per side, departing midrib at 55° angle, ± straight to collective vein, sunken above, raised below, interprimary veins sunken above, raised below, tertiary vein prominulous above, obscure below (drying prominent on both surfaces); collective vein arising from the first basal vein or from one of the lowermost primary lateral veins, sunken above, raised below, 4–8 mm from margin, sometimes the second basal vein running almost to apex. INFLORESCENCE erect, shorter than or equal to leaves; peduncle 16–40 cm long, 4–6 mm diam., terete, sometimes with a single ridge tinged reddish;

spathe thin, medium green (B & K Yellow-green 5/5), narrowly ovate to ovate-lanceolate, 5.5–7.5 cm long, 2–2.8 cm wide, narrowly acuminate at apex, rounded to subcordate at base, inserted at 45° angle on peduncle; spadix green heavily tinged purple or dark purple (B & K Blue-purple 2/10), 4–10.5 cm long, 5–9 mm diam. at base, 2–5 mm diam. at apex; flowers square 3–3.6 mm in both directions, the sides straight parallel to spirals, weakly to jaggedly sigmoid perpendicular to spirals; 5–6 flowers visible in the principal spiral, 6–7 flowers visible in the alternate spiral; tepals matte, weakly punctate, very minutely papillate, the lateral tepals 2.1–2.2 mm wide, the inner margin broadly rounded; pistils weakly emergent, green to purplish (paler than tepals); stigma linear, ca. 7 mm long, with large, clear droplets ca. 1 month before stamens emerge; lateral stamens emerging from the base, followed by alternates in rapid progression, leading stamens preceding the next in the series by 2 or 3 spirals; anthers white to pale yellow, ca. 0.7 mm long, 0.8 mm wide, held over pistil then retracting and held at sides of pistil; thecae ellipsoid, somewhat divaricate; pollen yellow, fading to white. INFRUCTESCENCE pendent, spathe deciduous; berries orange, obovoid, rounded at apex, 1.5 cm long, 8 mm diam., 6 mm thick; mesocarp fleshy, orange; seeds 2, greenish orange, flattened, ca. 9 mm long, 5 mm wide. Figs. 6, 7 and 10.

Anthurium andicola is endemic to Mexico, at 1,000 to 2,500 m elevation, occurring in both the Sierra Madre Oriental where it ranges from central Veracruz to northern Oaxaca and in the Sierra Madre del Sur south of Oaxaca City. One collection by MacDougall supposedly from La Gloria on the Chiapas-Oaxaca border is worthy of mention regarding its range and elevation. The only La Gloria near the border of the states of Oaxaca and Chiapas is near the Pacific Coast at an elevation of near sea level. This locality is out of place for *A. andicola* both geographically (being ca. 270 km east of the nearest other collecting locality) and altitudinally (all other collections from above 1,000 m). Yet the specimen differs little from collections made in the Sierra Madre del Sur (especially those from Pochutla). A collection from La Gloria (*MacDougall s.n.*, March 5, 1953) was designated the type of *A. oaxacamonticolum*. A *MacDougall s.n.* collection from La Gloria was studied that bears the date "Mar./53" (MEXU 110308) but it is uncertain whether this is the type because the type description describes a plant with larger leaves and inflorescences.

Anthurium andicola is recognized by its usually ovate, reniform or ovate-triangular leaves with prominently raised tertiary venation (especially on drying), and D-shaped or broadly sulcate petiole with sharp margins and green to dark violet-purple spadix. Both the petiole and the lower leaf blade surface are often covered with a thin waxy bloom. The species is among the most variable in Mexico and even within a single population variation in leaf shape can be great, varying from conspicuously lobed at the base to not at all lobed. Plants from central Veracruz in the type locality are uniformly ovate to broadly ovate with rounded lobes and an arcuate to parabolic or horse-shoe shaped sinus. Further south at the type locality of *A. macdougallii* the posterior lobes are often directed inward with the sinus almost reniform. The same variation occurs in the Sierra Madre del Sur but leaves there are often more diminutive with less pronounced posterior lobes and more frequently an arcuate sinus. Sometimes the anterior lobe is considerably reduced and almost rounded at the apex such as in the case of *Reko 6064* from Pochutla (Oaxaca) and *MacDougall s.n.* from La Gloria (Chiapas), which is the type of *A. oaxacamonticolum*. It has been placed in section *Belolonchium*.

The species is not easily confused with any other although some specimens, especially those with poorly developed posterior lobes from the southern cordillera, are similar to those of *A. chamulense*.

One specimen collected at an unknown locality in the Sierra de Oaxaca (September, 1961) and assigned a Matuda collecting number (*38275*) is sterile but probably is also *A. andicola*. This collection bears the herbarium name *A. glaucotitanioides* Matuda. The blade is thinner than most and does not have the pronounced venation of typical *A. andicola*.

The herbarium name *A. campii* A. D. Hawkes based on *Camp 2762* represents a form of *A. andicola* not much unlike the typical form from Veracruz, even though it was collected relatively near the type of *A. macdougallii*.

Matuda 38721, presumably collected near Mitla, SW of Oaxaca, has blades thinner and with less conspicuous venation than most *A. andicola*

FIGURES 6–9. 6–7. *Anthurium andicola* Liebm., *Croat 48215*.—8. *Anthurium angustispadix* Croat & Baker, *Croat 26600* (Type).—9. *Anthurium armeniense* Croat, *Croat 40905* (Type).

FIGURES 10–13. 10. *Anthurium andicola* Liebm., *Croat 48215*.—11–12. *Anthurium austinsmithii* Croat & Baker, *Croat 46915*.—13. *Anthurium* [illegible]

collections. The region was visited recently and turned up no obvious habitat for *Anthurium* so the live plants could not be investigated further. They are presumably only unusually thin-leaved collections of *A. andicola,* since that species occurs on both the Atlantic and Pacific slopes, but no other collections have been made in the vicinity of Mitla.

MEXICO. No other location, *Galeotti 6096* (BR); *Liebmann 22348* (MO, Photo). MÉXICO: S of Toluca de Lerdo, *Matuda 28025* (MEXU). OAXACA: no other location, *Galeotti 6056* (P); Cañon of Río Tlahuitoltepec, near Ayutla, *Camp 2762* (NY); Huatla de Jiménez, *Croat 48215* (MO); *Matuda 38620* (MEXU); ESE of Ixtlán de Juárez, *Graham & Frolich 1046* (MICH); La Gloria, *MacDougall s.n.* (MEXU); near Mitla, SW of Oaxaca, *Matuda 20321, 38721* (MEXU); District Pochutla, Cerro del Machete, *Reko 6064* (GH); Lachivia, *Matuda 38421* (MEXU); Sierra de Oaxaca, *Matuda 38275* (MEXU); SW of Sola de Vega, *Davidse 9665* (MO); S of Sola de Vega, *Rzedowski 21300* (ENCB, US, MICH); Tenango, *MacDougall 26027* (MEXU). VERACRUZ: Calcahualco, *Hernandez & Cedillo 1129* (MEXU, F); near Córdoba, *Valdivia 2137* (MEXU); NE of Cosocomatepec, *Croat 43933* (MO); SW of Huatusco, *Rzedowski 19049* (ENCB, MICH); Ixhuapan, *Cházaro 813* (MEXU); NW of Jalapa, *Ventura 4665* (CAS, ENCB); Munc. Juchique de Ferrer, *Hernandez 1585, 1596* (F); Orizaba, *Botterie 85, 135* (GH); *Matuda 1540* (MICH).

Anthurium angustispadix Croat & Baker, Brenesia 16 (Supl. 1): 23. 1979. TYPE: Costa Rica. Puntarenas: primary forest along Río Coto Brus in the vicinity of Alturas, 23 km N of La Unión (on Panamanian border), elev. ca. 1,500 m, *Croat 26600* (MO-2251852, holotype; CR, F, K, PMA, SEL, US, isotypes; Live at MO).

Epiphyte, sometimes secondarily terrestrial; stems 18–30 cm long, 1–1.5 cm diam., branching, creeping, elongate; internodes 0.8–2 cm long; roots numerous, dense, 3–4 mm thick, directed downward; cataphylls thin, 6–11 cm long, gradually long-acuminate at apex (the acumen 2–4 cm long and inrolled) drying tan, persisting, dilacerating. LEAVES spreading; petioles 5–22 cm long, 4–7.5 mm diam., narrowly, deeply, and acutely sulcate, rounded abaxially; geniculum 1.5–2 cm long; blades lanceolate to oblong-lanceolate, thin to medium thick, gradually long-acuminate at apex (the acumen acute or very minutely inrolled), acute to attenuate at base, 13–30 cm long, 4–7.5 cm wide, broadest slightly below the middle; the upper surface glossy, dulling with age, lower surface glossy or semiglossy; midrib raised, triangular above, diminishing toward apex, convexly raised below; primary lateral veins 11–16 per side, departing midrib at 55°–65° angle, sunken above, raised below, straight to arcuate-ascending, loop-connecting; collective vein arising from the base or the first or second pair of lateral veins, 3–4 mm from margin, sunken above, raised below. INFLORESCENCE erect-spreading; shorter to longer than leaves; peduncles 20–40 cm long, 1.5–3 mm diam., terete, equalling or longer than petioles; spathe medium green (B & K Yellow-green 5/10), linear-lanceolate, 4.5–8.5 cm long, 4–9 mm wide, broadest near the base, long-acuminate at apex, acute at base inserted at a 50°–70° angle on peduncle; stipe 3 mm long in front, 1 mm long in back, 4–5 mm diam., or spadix sessile; spadix greenish-yellow at base, paler at apex (B & K Yellow-green 8/5 to 6/7.5), 4.5–10 cm long, 3–6 mm diam. at base, 2–4 mm diam. at apex; flowers rhombic, 1.7–2.8 mm wide in both directions, the sides sigmoid; 5–6 flowers visible in the principal spiral, 5–10 flowers visible in the alternate spiral; tepals glossy to matte, papillate, green to greenish-yellow, brown in fruit, the lateral tepals 0.8–1 mm wide, the inner margin thin, turned up against pistil; pistils slightly emergent, green, at first covered by tepals and flat, rapidly emergent into a pointed mound; stigma 0.3–0.5 mm long, ellipsoid, brushlike, white, exserted, small droplet persisting for 1–2 days before stamens emerge, dry and gray when stamens emerge, usually not emerging in the apical half to third of spadix; stamens emerging rapidly from the base in a regular sequence, laterals first followed by alternates, held at the side of pistil, sometimes contiguous; anthers pale yellow, 0.2–0.3 mm long, ca. 0.4 mm wide; thecae ellipsoid, prominently divaricate, opening bowl-shaped; pollen orange-yellow, fading creamy white; strong sweet aroma present when stigma droplets appear and continuing while pollen is fresh. INFRUCTESCENCE spreading-pendent; the spathe green, intact; spadix 5–9 cm long; berries obovoid to depressed-globose, almost flat at apex, pale yellow-green, to 5 mm long; mesocarp watery, clear, sweet; seeds 2, pale green, flattened, to 2.8 mm long and 2.5 mm wide, each enveloped in a clear, gelatinous substance to 4 mm long. Fig. 8.

Anthurium angustispadix is known from eastern Costa Rica and western Panama at elevations from 100 to 1,500 m in premontane wet and tropical wet forest life zones.

The species is perhaps best placed in section

Xialophyllium and is recognized by its slender elongate stems with weathered, tan to pale brown cataphylls; its lanceolate leaves with a narrowly cuneate or attenuate leaf base; and its greenish-yellow, relatively long and slender, tapering spadix with pale yellow-green berries. It is not easily confused with any other species.

The species often branches from near the base in pots in the greenhouse. Plants sometimes set seed in the greenhouse without apparent manipulation.

COSTA RICA. PUNTARENAS: 10–15 km ENE of La Unión, *Utley 4802* (DUKE); cloud forest above Wilson's Finca, 6 km S of San Vito de Java, *Raven 20877* (F); Finca Alturas, NE of Sabilito, *Croat 44381* (MO); along Río Coto Brus, 23 km N of La Unión, *Croat 26600* (CR, F, K, MO, PMA, SEL, US), *26650, 26690* (MO); between Río Cotón and Río Negro (ca. 15 km from Sabalito) near Las Alturas lumber camp, *Burger & Matta 4553* (CR, F, NY); E of Las Cruces, 5–6 km S of San Vito on and around the property of Robert Wilson, *Burger & Matta 4437, 4455* (F); near Cañas Gordas, *Pittier 11127* (US).

Anthurium armeniense Croat, sp. nov. TYPE: Guatemala. San Marcos: ca. 2 km from Finca Armenia above San Rafael, 1,100–1,250 m, *Croat 40905* (MO-2599479, holotype; Live at MO).

Planta epiphytica; cataphyllum persistens intactum, brunneum; petiolus 19–28 cm longus; lamina ovata, 20–40 cm longa, 11.5–21 cm lata, basi cordata profunde; inflorescentia erecta aut effusa; spatha alba; spadix caesius aut roseus, 3–5.7 cm longus, fragrans; tepala marginibus elevatis; baccae aurantiacae.

Epiphyte; stems 1.5 cm diam.; leaf scars ca. 1.5 cm wide; roots 4–5 mm diam., descending; cataphylls subcoriaceous, 7 cm long, rounded to emarginate and cuspidate at apex, drying reddish-brown and persisting intact. LEAVES erect-spreading; petiole 19–28 cm long, 4–6 mm diam., terete; geniculum 2–3 cm long; blades narrowly ovate, gradually acuminate and downturned at apex, deeply lobed at base, 20–40 cm long, 11.5–21 cm wide, broadest at middle; anterior lobe 5–15 cm long, the margins broadly rounded; posterior lobes 5–12 cm long, directed downward to inward; sinus usually spathulate sometimes hippocrepiform, acute to rounded at apex; both surfaces semiglossy, the upper surface with ± conspicuous, minute, linear, raphide cells; midrib obtusely raised above, weakly sunken at apex, raised on lower surface; basal veins 4–6 pairs, the second to third pairs coalesced ca. 1.5 cm, the fourth to sixth coalesced ca. 2.8 cm, raised above and below, diminishing and flat at collective vein; primary lateral veins 2–4 per side, flat above, sunken below, departing midrib at 55°–60° angle, curved to margin, loop-connected; collective vein arising from the first basal vein, 4–15 mm from margin. INFLORESCENCE erect or spreading; peduncle 11.5–23 cm long, 2–3 mm diam., terete, as long as or longer than petioles; spathe white, narrowly ovate-elliptic or lanceolate-oblong, 4.5–9(12) cm long, 1.9–3 cm wide, broadest near base, long acuminate, green at apex, obtuse to acute at base, decurrent ca. 2 mm, inserted on peduncle at 70° angle; the stipe 2 cm long in front, 3–5 mm long in back, usually curved; spadix pale lavender (B & K Purple 6/5), fading to pink (B & K Red-purple 6/2.5) at anthesis, 3–5.7 cm long, 7–9 mm diam. at base, 6–7 mm diam. at apex, the flowers rhombic to weakly 4-lobed, 2.1–2.9 mm long, 2.8–3.6 mm wide, the sides straight to weakly and irregularly sigmoid, ca. 6 flowers visible in the principal spiral, 9 flowers visible in the alternate spiral; the tepals matte; lateral tepals 1.6–1.9 mm wide, the inner margins straight to convex; pistils white, emergent ca. 0.5 mm, the stigma broadly elliptic, whitish, brushlike with short papillae exserted above pistil; first lateral stamens emerging irregularly throughout, followed rapidly by second lateral stamens then alternates in rapid succession; anthers white, broadly ovate, 0.5–0.8 mm long, 0.8–1.4 mm wide; thecae broadly ovate, shallowly cupular; pollen white, abundant, strong sweet lilac scented. INFRUCTESCENCE pendent; spathe greenish-white, spadix 18 cm long, 3.5 cm diam., with berries exserted ca. 1 mm (early stages); berries obovoid, style dark, beaked at apex, pale orange (B & K Yellow-red 8/7.5), 1.2–1.5 cm long, 6–8 mm wide; mesocarp orange, juicy, gelatinous with numerous silvery raphide cells; seeds (1)2, ovoid-ellipsoid, pale whitish-green, darker green at base, reddish-brown at apex, weakly flattened, 4.5 mm long, 3–3.2 mm wide, 1.4–2.2 mm thick, surrounded by sticky, gelatinous, translucent substance, more prominent at lateral margins, extending beyond ends. Figs. 9 and 14.

The species is known only from the type locality from 1,100 to 1,600 m in moist to wet forests on steep slopes in southwestern Guatemala in the Department of San Marcos.

The species is a member of section *Calomystrium* and is recognized by its ovate-cordate moderately coriaceous leaves with raphide cells

evident on upper surface and by its thick, persistent cataphylls that dry reddish-brown, but especially by its pale lavender to pink fragrant spadix that has a distinctly bumpy surface owing to the slightly upturned edges of the tepals. The species also is characterized by its white spathe.

It is confused with *A. huixtlense*, which has similar leaves and cataphylls (both are in the section *Calomystrium*), but that species generally has a greenish spathe and a spadix that varies from white to lavender, and has tepals more nearly level with the surface of the spadix so that it does not have the bumpy appearance. In addition, *A. huixtlense* lacks the strong lilac scent of *A. armeniense*.

GUATEMALA. SAN MARCOS: Finca Armenia above San Rafael, *Croat 40905, 40923* (MO).

Anthurium austinsmithii Croat & Baker, Brenesia 16 (Supl. 1): 25. 1979. TYPE: Costa Rica. Alajuela: San Luis de Zarcero, elev. 1,450 m, *Austin Smith 637* (NY, holotype; F, isotype).

Epiphyte; roots numerous, slender, green drying grayish; stem moderately elongate, ca. 1 cm diam., 16–20 cm long, scurfy; cataphylls 2–2.5 cm long, drying dark reddish-brown, persisting as linear fibers. LEAVES spreading; petioles subterete, narrowly sulcate, 4–22 cm long, 2–4 mm diam.; geniculum 7–20 mm long; blades subcoriaceous, oblong-lanceolate, 11–21 cm long, 3–6.5 cm wide, long-acuminate at apex (the acumen flat), obtuse to acute (rarely attenuate) at base, broadest at or below the middle, the margin revolute on drying; both surfaces semiglossy, lower surface dark glandular-punctate; midrib acutely raised above, diminished and sunken toward apex, convexly raised below; primary lateral veins 7–15 per side, departing midrib at 45° angle, ± straight to the collective vein, slightly sunken above, prominulous below; interprimary veins sunken above, scarcely visible below; collective vein arising from the base, 4–8 mm from the margin, about equally as prominent as the primary lateral veins, sunken above, prominulous and darker below. INFLORESCENCE erect-spreading, equalling or exceeding the leaves; peduncle terete to sharply angulate, 2–3-ribbed, sometimes with only one rib, 21–25 cm long, 2–3 mm diam.; spathe pale green, lanceolate, 2.5–3 cm long, 4–8 mm wide, broadest just above the base, acuminate at apex, rounded at base, inserted at ca. 30° angle on the peduncle; spadix sessile, pale greenish-yellow, 5–7.5 cm long, 3–4 mm diam. at base, 2–2.5 mm diam. at apex, green at anthesis, becoming violet-purple; flowers rhombic, 3.3–3.5 mm long, ca. 2 mm wide, the sides ± straight; ca. 3 flowers visible in the principal spiral, ca. 5 flowers visible in the alternate spiral; tepals semiglossy, the lateral tepals 2–2.5 mm long, the inner margin broadly rounded to straight; pistil green soon turning purple, emergent to 0.5–0.6 mm; stigma elliptic; stamens emerging from the base in a slow complete progression, the laterals preceding the alternates by no more than 2 spirals, held above tepals and against pistil then retracting to edge of tepals, scarcely visible after anthesis; anthers 0.3 mm long, 0.7 mm wide; thecae ovate-elliptic, divaricate. INFRUCTESCENCE often developing berries only in the basal half of the spadix, berries subglobose to depressed-globose, ca. 7 mm diam., white tinged with violet-purple at apex, with a circular depression around the style ca. 2 mm diam.; locules 2, with 3 seeds per locule; seeds narrowly ovoid, 2.5–2.6 mm long, 1.3–1.5 mm wide, 1.1–1.3 mm thick, pale brown, weakly flattened to subterete in cross-section, smooth. Figs. 11 and 12.

Anthurium austinsmithii is known only from Costa Rica in lower montane rain, lower montane wet, lower montane moist, and premontane wet forest, primarily on the Atlantic slope at elevations of 1,200 to 1,560 m.

The species is a member of section *Porphyrochitonium* and can be distinguished by its acuminate leaf blades, conspicuously punctate on the lower surface which dry a dirty gray, slender spadix with ca. 3 flowers visible in the principal spiral and by its whitish berries tinged with purple-violet bearing a circular depression at the apex.

Anthurium austinsmithii is similar to *A. acutangulum, A. durandii,* and the species allied to them. It is also similar to *A. alatipedunculatum* because of its angulate peduncle, but the latter species also has a triangular petiole and is known currently only from the Osa Peninsula at much lower elevations than *A. austinsmithii.*

COSTA RICA. ALAJUELA: San Luis de Zarcero, *Austin Smith 637* (F, NY); *1332* (NY); one mile S of La Balsa de San Ramón, *Lent 3524* (F, MO): road from Zapote to Santa Elena, ca. 1 km S of Zapote, *Utley 4663* (DUKE); along Hwy. 15 between Naranjo and Quesada in vicinity of Laguna, 3.2 miles N of Zapote, *Croat 46915, 46921* (MO). HEREDIA: 4 miles N of Vara Blanca, *Croat 35570* (MO); 7.5 km N of Vara Blanca, *Croat 36046* (MO).

Anthurium bakeri Hook. f., Bot. Mag. pl. 6261. 1876. TYPE: Costa Rica. *Bull s.n.* (K).

Anthurium turrialbense Engl., Bot. Jahrb. Syst. 25: 406. 1898. TYPE: Costa Rica. Cartago: Turrialba, 500 m, *Donnell Smith 4978* (B).

Epiphyte, stems less than 10 cm long, 1.5 cm diam.; roots moderately slender; leaf scars ca. 1.7 cm wide; cataphylls coriaceous, 3–6 cm long, acuminate at apex (the acumen apiculate to 2 mm), drying brown, persisting as fibers. LEAVES erect to spreading; petioles (3)11–17 cm long, to 5 mm diam., subterete to sharply sulcate; geniculum 1–1.5 cm long; blades narrowly elliptic-lanceolate to narrowly oblanceolate, 19–55 cm long, 2.8–9 cm wide, broadest at middle, acuminate at apex, narrowly rounded at base; upper surface matte, lower surface paler and matte with reddish-brown glandular punctations; midrib convexly raised below; primary lateral veins nearly obscure, flat, departing midrib at 45° angle, straight to collective vein; collective vein arising from base, sunken, significantly more prominent than the primary lateral veins, continuous to apex of leaf, 2–4 mm from margin. INFLORESCENCE erect-spreading, much shorter than leaves; peduncle 5.5–30 cm long, 3–5 mm diam., half as long or as long as petioles; spathe coriaceous, pale yellow-green (B & K Yellow-green 9/10), the edges sometimes tinged with purple, 2–5.5 cm long, 7–28 mm wide, oblong-lanceolate, inserted at ca. 60° angle on peduncle, obtuse at apex and base; stipe 3 mm long, 2 mm diam.; spadix creamy white (B & K Yellow-red 9/5), 2–11 cm long, 5–15 mm diam. at base, 4.5–12 mm diam. at apex; flowers square to 4-lobed, 1.6–3.5 mm long, 1.7–3.2 mm wide, the sides jaggedly sigmoid, 7–8 flowers visible in the principal spiral, 5–6 flowers visible in the alternate spiral; tepals glossy, minutely papillate, lateral tepals 1.5 mm wide, the inner margin convex; pistils not emergent; stigma minute, slitlike, ca. 0.1 mm long, droplets apparent before stamens emerge; stamens emerging in an irregular pattern, usually lateral stamens first followed by alternates, anthers scarcely exposed, pushing pollen out around pistil, white, ca. 0.2 mm long, 0.3 mm wide; pollen white. INFRUCTESCENCE erect, spathe reflexed against peduncle; spadix 7.5–8.5 cm long, 1.2–1.4 cm diam.; berries red, pointed at apex, obovoid ca. 6 mm long; mesocarp juicy, pulpy, transparent with numerous oblong raphide cells; seeds 2, ovoid, cream-colored, flattened, 3.2 mm long, 2 mm wide, 1.2 mm thick, enveloped by a gelatinous substance extending below the base. Figs. 13 and 15.

The species is known from Guatemala to Colombia in wetter parts of tropical moist, premontane wet, and tropical wet forest at elevations from sea level to 660 m. In Panama, the species ranges to 1,000 m elevation. In Colombia it is known from a single collection from Norte de Santander (Camp 84 on Pipeline, 600 m), *M. B. & R. Foster 1716* (A).

Anthurium bakeri can be distinguished by its moderately thin, elliptic-lanceolate blades that are reddish-brown punctate on the lower surface and have many weak primary lateral veins and conspicuously sunken collective veins. The lower leaf surface usually dries much paler than upper surface, sometimes yellowish, contrasting sharply with the green upper surface. Other distinguishing features include the creamy white, almost cylindrical spadix and bright red berries. The species is a member of section *Porphyrochitonium*.

BELIZE. BELIZE DISTRICT: near Quamina Creek, *Gentle 3426* (MICH). STANN CREEK DISTRICT: Middlesex, *Gentle 2898* (MICH); Silk Grass Creek, *Gentle 2626* (K, MICH, NY); South Stann Creek, *Schipp S-16* (MICH); north of Victoria Peak, *Gentry 8037* (MO). TOLEDO: Columbia Forest Station, *Croat 24225* (MO); *Proctor 36124* (MO); Maya Mountains, *Boutin & Schlosser 5013, 5114* (MO); San Jose, *Croat 24453, 24359* (MO).

COSTA RICA. ALAJUELA: N of Ángeles Norte, *Luteyn 3381* (DUKE); NNE of Bijagua, *Croat 36283, 36326, 36430* (MO); *Utley & Utley 5335* (DUKE); south of Canalete, *Burger & Baker 9977* (DUKE, MO); Hacienda Santa María, *Liesner 5131* (MO); NW of New Volcan Arenal, *Taylor 11588* (NY); NE of Quesada, *Croat 46944* (MO). CARTAGO: Turrialba, *Croat 994* (MO); *LePoole s.n.* (U); near Tuis, *Luteyn 749* (DUKE). GUANACASTE: NW of Lake Arenal, *Croat 259* (MO). HEREDIA: near Puerto Viejo, *Croat 35692, 35753A* (MO); *Jiménez 105* (MO); *Taylor 4549, 4572* (NY); Vara Blanca, *Skutch 3651* (MICH). LIMÓN: Hacienda Tapezco-Hacienda La Suerte, *Davidson & Donahue 8254* (MO); Finca Castilla, *Dodge & Goerger 9272* (MO). PUNTARENAS: Osa Peninsula, *Dodge & Goerger 10021, 10022, 10150* (MO); *Liesner 3097* (MO); Rincón de Osa, *Utley & Utley 1032* (DUKE). SAN JOSÉ: from San Isidro del General to Dominical, *Burger & Baker 10106* (MO).

GUATEMALA. ALTA VERAPAZ: vicinity Cubilhuitz, *Steyermark 44382* (NY); vicinity Laguna Sapalau, *Steyermark 44917* (MO); Oxec Rd., *Croat 41606, 41653* (MO). IZABAL: vicinity Exmibal, *Jones & Facey 3280A* (NY). PETÉN: NW of Chinajá, *Steyermark 45481* (MICH).

HONDURAS. ATLÁNTIDA: La Ceiba, *Yuncker et al. 8739* (MO, NY); Lancetilla, *Chickering 16, 104, 163* (MICH); Lancetilla Valley, *Croat 42638* (MO); *Web-*

FIGURES 14–17. 14. *Anthurium armeniense* Croat, *Croat 40923*.—15. *Anthurium bakeri* Hook. f., *Croat 34344*.—16. *Anthurium berriozabalense* Matuda, *Honolulu Botanic Garden 77-1275*.—17. *Anthurium berriozabalense* Matuda, *Croat 47715*.

ster et al. 12704 (DAV); *Yuncker 4960* (MICH, MO). COMAYAGUA: NW of Siguatepeque, *Molina 26062* (NY). GRACIAS A DIOS: vicinity Río Plátano, *Clewell & Cruz 4061* (MO). YORO: Coyolito, *Carleton 552* (US); *Yuncker et al. 8187* (NY, S).

MEXICO. CHIAPAS: Mun. of Las Margaritas, *Breedlove & McClintock 34076* (CAS).

NICARAGUA. CHONTALES: no other location, *Levy 1420* (P); N of Cuapa, *Neill 7471* (MO). MATAGALPA: Cerro Musún, *Neill 1808* (MO); E of Matagalpa, *Neill 2353* (MO). RIVAS: Volcán Maderas, *Neill & Vincelli 3247* (MO); *Stevens 6507* (MO). ZELAYA: Caño Zamora, *Stevens 8824, 8826* (MO); Cerro El Inocente, *Neill 1906* (MO); *Stevens 6714* (MO); Cerro Waylawás, *Stevens 8756* (MO); SW of Colonia Naciones Unida, *Stevens 5023* (MO); trail from Colonia San José, NNE to Parcela, *Stevens 9008* (MO); Colonia Agricola Yolaina, *Stevens 4827* (MO); *Stevens et al. 6437* (MO); Río Rama, *Proctor et al. 27414* (LL, NY); *Stevens 8909* (MO); west of Río Ulí, *Neill 1927* (MO); vicinity of Siuna, *Neill 4499* (MO); *Neill 4225* (MO); near Tala Has and Puente Mango, *Stevens 7620* (MO).

Anthurium beltianum Standl. & L. O. Wms., Ceiba 3: 103. 1952. TYPE: Nicaragua. Dept. of Jinotega: mountains east of Jinotega, along trail to Cerro la Cruz, elev. 1,050–1,350 m. *Standley 10255* (F, holotype; EAP, isotype).

Terrestrial; stems thick, to 4 cm diam., leaf scars 4 cm wide; roots sparse, descending, tan; cataphylls coriaceous, 4–12 cm long, caudate and apiculate at apex, drying yellow (B & K Yellow 5/10), persisting as moderately coarse longitudinal fibers. LEAVES erect-spreading; petioles 13–73 cm long, 5–8 mm diam., subterete, shallowly and bluntly sulcate, sometimes merely flattened adaxially; geniculum 1.5–2.5 cm long; blades subcoriaceous, triangular-ovate to ovate, acuminate at apex, deeply lobed at base, 14–51 cm long, 8–36 cm wide, broadest at point of petiole attachment, the margin undulate; posterior lobes 5–18 cm long from sinus to tip, the sinus hippocrepiform to triangular, acute to round at apex; both surfaces matte to semiglossy, sometimes with punctiform or linear raphide cells (more conspicuous on dry specimens); midrib raised above and below; basal veins 5–6 pairs, the first and second free, the remaining coalesced 2.7–4 cm, raised above and below; posterior rib turned up along the outer margin; primary lateral veins 4–8 per side, departing midrib at 40°–55° angle, flat to weakly raised above, raised below; interprimary veins flat above, raised below; lesser veins scarcely visible; collective vein arising from the first basal vein or one of the primary lateral veins, 1–2.5 cm from margin, flat above, raised below. INFLORESCENCE erect-spreading; peduncle 20–67 cm long, 3–6 mm diam., slightly curved near base of spadix, shorter to longer than leaves; spathe green (B & K Green 6/2.5), subcoriaceous, narrowly ovate or boat-shaped, 8–15 cm long, 2–5 cm wide, broadest just above middle, long-acuminate at apex, decurrent and clasping at base, inserted at 65°–80° angle on peduncle, held behind and hooding spadix; spadix pale green (B & K Green 7/2.5), glaucous, 6.5–12 cm long, 5–8 mm diam. at base, 4–5 mm diam. at apex, slightly curved just below middle so that the tip turns down; flowers 4-lobed, 2–3 mm long, 2.5–3.5 mm wide, the sides jaggedly sigmoid; 4–5 flowers visible in the principal spiral, 5–10 flowers visible in the alternate spiral; tepals matte, densely and minutely papillate, with droplets, lateral tepals 1.5 mm wide, the inner margin convex; pistils emergent, bright green; stigma slitlike with blunt papillae and a large droplet for 3 or 4 days before first stamens emerge; stamens emerging very slowly in a complete sequence from base, held in tight circle around pistil just above the tepals; anthers pale yellow, slanting over pistil before opening, ca. 0.6 mm long, 1.1 mm wide; thecae ellipsoid, somewhat divaricate; pollen pale yellow, fading white. INFRUCTESCENCE pendent, spathe persisting; berries obovoid-ellipsoid, yellow to yellow-orange, 13–15 mm long, 9–11 mm wide; pericarp thick, darker colored and lacking raphide cells near apex, numerous granular raphide cells in the lower half; mesocarp juicy, fragrant, sweet; seeds 1–2, semicircular to broadly ellipsoid, brown with numerous minute granular projections on surface, flattened, 8–9 mm long, 8–9 mm wide, 3 mm thick, encased in a thin envelope. Figs. 18 and 19.

Anthurium beltianum is endemic to central Nicaragua in the departments of Jinotega and Matagalpa at elevations of 1,000 to 1,500 m in premontane wet forest life zones, on limestone outcrops.

The species was named in honor of the famous English naturalist Thomas Belt, author of the "The Naturalist in Nicaragua." It is a member of section *Calomystrium* and is recognized by its moderately thick, ovate-cordate leaves with an obovate or hippocrepiform sinus, but especially by its semi-erect inflorescence with the moderately short, tapered, pale green spadix directed downward and by its lanceolate-elliptic to narrowly ovate spathe, which curves outward forming a protective covering above the spadix.

FIGURES 18–21. 18–19. *Anthurium beltianum* Standl. & L. O. Wms., *Croat 43003.*—20–21. *Anthurium brenesii* Croat & Baker, *Croat 46923* (Type).

Anthurium beltianum is similar to *A. cotobrusii,* which has generally similar leaves and inflorescences but does not have the hooded inflorescences of *A. beltianum.*

NICARAGUA. JINOTEGA: vicinity of Jinotega, *Croat 43003* (MO); *Standley 10255, 10359, 10883* (F); *Williams et al. 24733* (F); MATAGALPA: vicinity of Aranjuez, *Neill 3020, 3452* (MO); Finca Santa María de Ostuma, *Williams et al. 27887* (MO).

Anthurium berriozabalense Matuda, Anales Inst. Biol. Univ. Nac. México 25: 214. 1954. TYPE: Mexico. Chiapas: Las Vistas north of Berriozábal, 1,250 m elev., *Miranda 6707* (MEXU, holotype).

Terrestrial on rocky, steep slopes to 0.6 m tall; stems 10 cm long, 1.5–3 cm diam.; leaf scars ca. 1.5 cm wide; roots ca. 5 mm thick, directed downward; cataphylls subcoriaceous, 3–5 cm long, acute at apex, the acumen minutely apiculate, drying light brown (B & K Yellow 4/5), persisting intact at apex, splitting into linear fibers at base. LEAVES erect to spreading; petioles 13–56 cm long, 3–7 mm diam., subterete, weakly flattened adaxially; geniculum 1.5–2 cm long broadly and shallowly sulcate; blades triangular, acuminate at apex, broadly lobed at base, 12–33 cm long, 11–23 cm wide, broadest at base; anterior lobe 9–16 cm long; posterior lobes 12–18 cm long, directed outward; sinus triangular to parabolic to sometimes hippocrepiform; upper surface semiglossy to glossy, lower surface semiglossy, the midrib convexly raised above and below, diminishing at apex above; basal veins 4–5 pairs, the first and sometimes the second free, second to fourth coalesced ca. 1.5 cm, third to fifth coalesced 2.3–4 cm, raised in weak valleys above, raised below; posterior ribs curved, naked, the outer margin upturned; primary lateral veins 4–5 per side, departing midrib at 45°–50° angle, raised or flat above, raised below; collective vein arising from uppermost basal vein (sometimes with lower basal veins loop-connecting to the collective vein), sunken above, raised below, 6–10 mm from margin. INFLORESCENCE spreading to erect, shorter than the leaves; peduncle 16–40 cm long, 2–4 mm diam., terete, sometimes tinged with violet-purple, longer than the petioles; spathe medium thick, green tinged with purple at margins, lanceolate to oblong-lanceolate, 4.5–9 cm long, 0.9–2.7 cm wide, broadest at base, acuminate at apex, clasping to truncate or rounded at base, inserted at 45°–60° angle on peduncle; spadix green (B & K Yellow-green 5/7.5), 5–10 cm long, 7–9 mm diam. at base, 2–3 mm diam. at apex; flowers square or rhombic, 3–5 mm long, 3–4 mm wide, the sides ± straight to jaggedly sigmoid; 3–5 flowers visible in either spiral; tepals matte, green, inconspicuously punctate, minutely papillate, tinged with violet at margins, sparse droplets appearing when anthers are open, lateral tepals 1.5–2.5 mm wide, inner margins straight; pistil scarcely emergent, green, densely purple spotted; the stigma oblong, shallow, green, 0.8–1 mm long, opening with minutely exserted papillae, small droplets apparent for 7–10 days, dry and black for 2 or 3 days before first stamens emerge; stamens emerging ± rapidly from the base, the second, third, and fourth stamens emerging soon after leading stamen; anthers brown, held on short filaments that quickly retract, anthers held at edge of pistil but not contiguous; thecae ellipsoid, divaricate; pollen yellow, fading to white. INFRUCTESCENCE pendent; spathe withered; spadix to 10 cm long, 20 mm diam.; berries orange (B & K Yellow-red 7/5), broadly obovoid, round at apex with a conspicuous indentation, 8–11 mm long, 7–10 mm wide; pericarp transparent, somewhat thickened, lacking raphide cells; mesocarp fleshy, juicy, with numerous raphide cells; seeds 1 or 2, flattened on one side if 2, ellipsoid in cross-section if only one, pale green, 6–8 mm long, 4.5–5(9) mm wide, 3.2–3.5(6.5) mm thick. Figs. 16, 17, and 26.

Anthurium berriozabalense is restricted to Mexico and is known for certain only from northeastern Chiapas at 1,000 to 1,300 m. A collection from eastern Oaxaca (*MacDougall 311*) from Río Grande (presumably near Matías Romero) is probably also this species. The forest type near El Bosque where I have collected the species is "bosque caducifolia" and the forest type where it has been collected north of Berriozabal is "selva baja caducifolia."

The species is tentatively placed in section *Belolonchium* and is recognized by its semiglossy sagittate leaf blades with long, slender, posterior lobes that are usually as long or longer than the anterior lobes, and also by its green spathe and spadix and subglobose orange berries.

Anthurium berriozabalense is perhaps related to *A. seleri,* a more wide ranging species whose range overlaps that of *A. berriozabalense.* Forms of *A. seleri* with long, slender posterior lobes have been confused with *A. berriozabalense* but they can be distinguished from *A. berriozabalense* by

FIGURES 22–25. 22. *Anthurium brownii* Mast., *Croat 37840*.—23. *Anthurium brownii* Mast., *Croat 10389*.—24. *Anthurium caperatum* Croat & Baker, *Croat 43358*.—25. *Anthurium caperatum* Croat & Baker, *Croat 48664*.

FIGURES 26–29. 26. *Anthurium berriozabalense* Matuda, *Croat 47715*.—27. *Anthurium brenesii* Croat & Baker, *Croat 46923* (Type).—28. *Anthurium burgeri* Croat & Baker, *Burger & Baker 10096* (Type).—29. *Anthurium carnosum* Croat & Baker, *Croat 48619*.

the much longer (or at least equally as long) anterior lobes and by the anterior lobe and posterior lobes forming a broad concave edge. In *A. berriozabalense,* the margin is either straight or convex and the posterior lobes are usually as long or longer than the anterior lobes. In addition, the leaves of *A. berriozabalense* are thin whereas the leaves of *A. seleri* are subcoriaceous. Still another difference is that the collective vein of *A. berriozabalense* usually arises from the uppermost basal veins or has the lower basal veins conspicuously loop-connected with the collective vein. In *A. seleri* the collective vein arises from one of the lowermost basal veins and extends rather uniformly along the margin of both the posterior lobes and the anterior lobe to the apex.

In the type description Matuda discussed the similarity of *A. berriozabalense* to *A. umbrosum* but these two species are not at all similar except that both have orange berries.

MEXICO. CHIAPAS: vicinity Berriozábal, *MacDougall 445* (MEXU); *Miranda 6707* (MEXU); vicinity Simojovel de Allende, *Croat 47715* (B, CAS, F, K, M, MEXU, MO, NY, RSA, SEL, US, VEN). OAXACA: Río Grande, *MacDougall 311* (MEXU).

Anthurium brenesii Croat & Baker, Brenesia 16 (Supl. 1): 28. 1979. TYPE: Costa Rica. Alajuela: along Hwy. 15 between Naranjo and Quesada, 3.2 miles N of Zapote, 1,560 m, *Croat 46923* (MO-2682420, holotype; COL, CR, DUKE, F, GH, K, NY, PMA, RSA, SEL, US, VEN, isotypes; Live at MO).

Epiphyte; stems short, 1.5–2.5 cm diam.; roots moderately few, to ca. 5 mm diam.; cataphylls moderately thick, 10–25 cm long, acuminate at apex, tinged red at margins, weathering into fibers, drying light brown. LEAVES pendent; petioles 14–45 cm long, ca. 6 mm diam., terete; geniculum to 1.5 cm long; blades oblong, moderately coriaceous, abruptly to gradually short-acuminate at apex, acute to weakly attenuate at base, 32–68 cm long, 6–10.3 cm wide, broadest near the middle, the midrib raised above and below; the primary lateral veins 13–15 per side, departing midrib at 55° angle, sunken above, prominulous below; collective vein arising from the base, 2–5 mm from the margin, sunken above, raised below. INFLORESCENCE erect or pendent, shorter than the leaves; peduncle (10)28–43 cm long, 4–5 mm diam., terete, shorter or longer than petioles; spathe moderately thick, medium green sometimes tinged reddish at anthesis, ovate to ovate-elliptic, 5.5–8.5 cm long, 3.5–5.5 cm wide, broadest from 1 cm above the base to about the middle, acute to rounded and apiculate at apex, cordate and somewhat clasping at base, inserted at 25°–40° angle on peduncle, ± erect and held close to spadix or at ca. 45° angle to peduncle; spadix sessile or subsessile, green, reddish-brown to red-violet, 7–8 cm long, to 8 mm diam., at base, to 6 mm diam. at apex; flowers square to weakly 4-lobed, 1.7–2.5 mm long in both directions; 6–10 flowers visible in the principal spiral, 6–9 flowers visible in the alternate spiral; the lateral tepals to 1.2 mm wide, the inner margin concave, pistil green scarcely emergent, the stigma oblong, 0.5–0.6 mm long; stamens emerging rapidly throughout, lateral stamens first, quickly followed by alternate stamens, exserted on short, translucent filaments, retracting to hold anthers just above the margins of the tepals; anthers orange, ca. 0.6 mm long, 0.8 mm wide; thecae ovate-ellipsoid, slightly divaricate; pollen orange, faintly spicy scented at anthesis. INFRUCTESCENCE spreading to pendent, the spathe usually withered, the spadix to 9 cm long, 2 cm diam.; berries exserted ca. 1 mm, before maturity, obovoid, flattened, orange (B & K Yellow-red 7/5), 9–11 mm long, 5–7.5 mm diam., rounded at apex; mesocarp juicy with sparse, thick raphide cells; seeds 2 (rarely 1), tan, 3–4.5 mm long, 2.2–3 mm wide, 1.8–2.2 mm thick, enveloped in almost translucent (tinged orange) casing, ca. 10 mm long and as wide as the seed. Figs. 20, 21, and 27.

Anthurium brenesii is presently known only from the Cordillera Central in the Province of Alajuela between San Ramón and Quesada at 1,000 to 1,560 m elevation.

The species is related to *A. protensum* with which it shares similar leaf texture and cataphylls, and similar altitudinal range. It differs from that species, however, by its abruptly acuminate leaf blades, its short, broad spathe, which is subcordate at the base, and its shorter, broader spadix. It is also similar, especially vegetatively, to *A. prolatum,* but differs in having much shorter, broader leaves. It is placed in section *Pachyneurium.*

COSTA RICA. ALAJUELA: La Palma de San Ramón, *Brenes 5738* (F); Cordillera Central ca. 15 km N of Zarcero, *Williams et al. 29034* (F); along Hwy. 15 between Naranjo and Quesada, 3.2 miles N of Zapote, *Croat 46923* (COL, CR, DUKE, F, GH, MO, NY, PMA, RSA, SEL, US, VEN).

Anthurium brownii Mast., Gard. Chron. 6: 744, Figs. 139, 140. 1876. TYPE: Colombia (Nueva Granada). *Wallis s.n.* (K, exact status unknown).

Epiphyte; stems short, 2.5–3 cm diam.; roots few, thick, puberulent to densely velutinous; cataphylls coriaceous, 9–15 cm long, caudate-acuminate at apex, drying reddish-brown (B & K Yellow 4/2.5), persisting ± intact, ultimately weathering to a network of fibers at base. LEAVES erect to spreading; petioles 13–100 cm long, 3–10 mm diam., subterete, shallowly and bluntly sulcate; geniculum 2–2.5 cm long, sometimes tinged red-violet (B & K Red-purple 4/10); blades narrowly ovate-triangular, moderately thick, 15–66 cm long, 11–48 cm wide, broadest at base, gradually acuminate at apex (the acumen flat, apiculate), prominently lobed at base; anterior lobe 11–40 cm long, the margins straight to convex; posterior lobes 4–13 cm long, directed sharply upward; the upper surface matte to semi-glossy, lower surface paler; midrib convexly raised above, sometimes tinged reddish, sunken at apex, acutely raised below; basal veins 5–6 pairs, the first to fourth coalesced 2–6 cm, the posterior rib naked, upturned along outer margin; primary lateral veins 4–8 per side, departing midrib at 25°–35° angle, raised in valleys at base above, sunken at apex, raised below; lesser veins visible but less prominent; collective vein arising from first basal vein or lowest primary lateral vein, 2–7 mm from margin. INFLORESCENCE erect, longer than leaves; peduncle 51–65.6 cm long, 4–6 mm diam., terete, green mottled with red-violet, longer than petioles; spathe lanceolate, green (B & K Yellow-green 6/10), 8–23 cm long, 1.5–4.5 cm wide, acuminate at apex, round to cordate at base; spadix stipitate to ca. 11 cm, violet-purple, 7–28 cm long, 4–15 mm diam.; flowers rhombic, 2.5–3.2 mm long, 2–3 mm wide, the sides straight to sigmoid; 7–10 flowers visible in the principal spiral, 5–12 flowers visible in the alternate spiral; tepals matte, punctate, minutely papillate, sometimes with droplets, lateral tepals 1.8–2 mm wide, the inner margin broadly rounded; pistils emergent; stigmas linear, ca. 0.5 mm long, large droplet apparent ca. 1 week before first stamens appear, turning glossy then gray and drying when anthers open; stamens emerging rapidly in a ± systematic progression from base, lateral stamens emerging in basal one third before alternates emerge, held in circle around pistil; anthers yellow or tinged purple, thecae moderately divaricate, pollen purple fading to white sometimes yellow, with a pungent fruity aroma at anthesis. INFRUCTESCENCE pendent-spreading, 38 cm long, 3 cm diam.; berries ellipsoid to obovoid, 5–8 mm long, ca. 5 mm wide, orange to red-orange (B & K Yellow-red 7/2.5); pericarp thick; mesocarp juicy; seeds 2, oblong, greenish-white, flattened with transparent sticky appendages at both ends, elongated at apex, rounded at base. Figs. 22 and 23.

The species is known from Costa Rica to Colombia at elevations from near sea level to 1,200 m. In Costa Rica the species occurs in premontane wet and tropical wet forest. In Panama it also occurs rarely in premontane moist and tropical moist forest.

The species was confused with *A. denudatum* Engl. from Colombia by Standley (1944) in the *Flora of Panama*, but that species has a peduncle much shorter than the petioles, as well as a shorter spadix.

Anthurium brownii is a member of section *Belolonchium* and is distinguished by its thick blades with usually undulate margins and reticulate veins that dry very prominent. The leaf tends to dry silver or grayish on both surfaces. Also distinctive are the long, slender, violet-purple spadix and the red-orange berries.

COSTA RICA. ALAJUELA: NNE of Bijagua, *Burger & Baker 9855* (F, MO). HEREDIA: vicinity Río La Paz Grande, *Croat 35859* (MO). PUNTARENAS: near Rincón de Osa, *Koch 5065* (MO). SAN JOSÉ: SW of San Isidro del General, *Utley & Utley 4926* (DUKE).

Anthurium burgeri Croat & Baker, Brenesia 16 (Supl. 1): 30. 1979. TYPE: Costa Rica. San José: ridges and steep slopes above Alfombra along road from San Isidro del General to Dominical (on Pacific coast) (9°18'N, 83°46'W), ca. 1,000 m, 19 November 1975, *Burger & Baker 10096* (F 1769194, holotype; CR, K, MO, US, isotypes; Live at MO).

Epiphyte or terrestrial on steep banks; stem short or long, 1–1.3 cm diam.; roots few, directed downward; cataphylls moderately thin, 6–14 cm long, blunt to acuminate at apex, drying brown (B & K Red-yellow 4/10), remaining intact, subsequently deciduous. LEAVES usually held ± erect to spreading; petioles 15–20 cm long, 4–6 mm diam. midway, terete; geniculum (0.5)1.5–2 cm long, weakly flattened adaxially; blades oblong-oblanceolate, moderately thick (drying

somewhat reddish-brown or gray with purplish splotches), gradually acuminate at apex, narrowly cuneate at base, 36–48 cm long, 6.8–8 cm wide, broadest at or just above the middle; upper surface glossy to semiglossy or matte, lower surface semiglossy; midrib prominently raised above and below, broad at the base, becoming acute and narrow, then diminished and sunken at apex above, obtusely angled, sometimes tinged reddish near the base below; primary lateral veins 10–20 per side, departing midrib at ca. 60° angle, ± straight to the collective vein, flat and somewhat obscure above, raised below; collective vein arising from near the base, more conspicuous than the primary lateral veins, 2–9 mm from margin, weakly sunken above, prominulous below. INFLORESCENCE spreading, as long as or longer than the leaves; peduncle 40–53 cm long, to 4 mm diam., terete, longer than petioles; spathe moderately thin, light green sometimes tinged purple at margins (B & K Yellow-green 7/10) oblong-lanceolate to lanceolate, 6.5–9 cm long, 1.3–2.3 cm diam., broadest near the base, acuminate-cuspidate at apex, rounded to weakly cordate and slightly clasping at base, the margins sometimes joining petiole at slightly different levels; spadix sessile, greenish-brown to purplish-brown (B & K Yellow 6/7.5), 9–12.2 cm long, 5–7 mm diam. at base, to 3 mm diam. at apex; flowers rhombic to weakly 4-lobed, 2–3 mm wide in both directions, the sides straight to weakly sigmoid; 5–9 flowers visible in either spiral; tepals weakly glossy to matte, pale yellow-green with purplish inner edges, pale punctate, with a few scattered droplets, lateral tepals 1–1.3 mm wide, the inner margin broadly convex to almost straight; pistils weakly emergent, greenish; stigma ellipsoid-circular, ca. 5 mm long, brushlike and exserted, dark violet-purple, with a conspicuous droplet appearing briefly, well before first anthers emerge, dry and dark when anthers emerge; stamens emerging promptly from near the middle of the spadix or from the base, held ca. 1 mm above the tepals at anthesis, the filament ca. 3 times longer than the anthers, soon retracting the anther to the level of the tepals; anthers yellow-brown, 0.4–0.5 mm long, 0.7–0.8 mm wide, not contiguous; thecae weakly divaricate, oblong-elliptic; pollen orange (B & K Yellow 8/2.5), drying tan to whitish, quickly disappearing. INFRUCTESCENCE pendent-spreading; spadix ca. 12 cm long, ca. 1.9 cm diam., bearing berries in the basal half only; berries narrowly ovate, 6–6.7 mm long, 3–3.4 mm wide, acute to narrowly rounded at apex, red-orange (B & K Yellow-red 5/2.5); pericarp red-orange; mesocarp gelatinous, pale orange, with numerous raphide cells; seeds 1 or 2, elliptic, pale yellow, sometimes weakly flattened, 3.2–3.5 mm long, 2–2.1 mm wide, 1.2–2 mm thick, surrounded by a sticky amber envelope. Fig. 28.

The species is known only from the type locality in Costa Rica in premontane rain forest.

Anthurium burgeri can be distinguished by its oblong-oblanceolate leaf blades with obscure primary lateral veins, and more or less straight, weakly depressed collective veins arising from near the base. The midrib on the lower surface is sometimes tinged reddish and the cataphylls turn brown and remain intact. The inflorescence is equal to or longer than the leaves and the spadix is greenish to purplish-brown with dark violet-purple stigmas. It does not seem to be closely related to any other species in Central America. The sectional placement of *A. burgeri* is as yet uncertain but is probably best placed in section *Xialophyllium* despite the fact that it may sometimes have short stems.

COSTA RICA. SAN JOSÉ: above Alfombra along road from San Isidro del General to Dominical, *Burger & Baker 10096* (CR, F, K, MO, US).

Anthurium caperatum Croat & Baker, Brenesia 16 (Supl. 1): 32. 1979. TYPE: Costa Rica. Heredia: vicinity of Bajo la Hondura, along road between Paracito and the Río Claro, 1,100–1,400 m elev.; *Croat 44518* (MO-2598657-58, holotype; CR, F, US, isotypes; Live at MO).

Epiphytic near the ground or terrestrial; roots (1)3–5 mm diam., directed outward and downward; stem 60–120 cm long, 2.5–5 cm diam.; leaf scars 2.5–4.5 cm wide, cataphylls coriaceous, green tinged with purple, 14–40 cm long, narrowly rounded at apex with a subapical apiculum ca. 3 mm long, drying pale brown, weathering into fine fibers. LEAVES erect-spreading; petioles 24–109 cm long, 6–15 mm diam., subterete, shallowly and bluntly sulcate; geniculum 1.5–5 cm long; blades ovate to narrowly ovate, subcoriaceous, usually weakly bullate, abruptly to gradually acuminate at apex, prominently lobed at base, 46–120 cm long, 30–69 cm wide, broadest at point of petiole attachment; anterior lobe 26–90 cm long, the margins ± straight; posterior lobes 12–30 cm long, flat or directed inward,

often overlapping, the sinus spathulate, obovate or hippocrepiform, broadly acute to obtuse or rounded at apex; upper surface semiglossy or almost matte; lower surface matte; midrib sharply raised in a weak valley above, diminished and sunken near apex, convexly raised below, sometimes weakly ribbed or striate; basal veins 4–9 pairs, (second) fourth to seventh coalesced (2)4.5–9 cm, raised above and below, the posterior rib stout, curved or nearly straight, naked, rolled up along the outer margin; primary lateral veins 9–18 per side, departing midrib at 55° angle, ± straight to slightly ascending to a weak collective vein, sharply raised in weak valleys above, raised below; collective vein usually arising from fourth or fifth basal vein, sunken above and raised below, 1–4(10) mm from the margin, loop-connecting the basal and primary lateral veins. INFLORESCENCE erect, much shorter than the leaves; peduncle 6–54 cm long, 8–13 mm diam., subterete or terete, as long as petioles; spathe thin, pale green (B & K Yellow-green 7/10), lanceolate-oblong, 10–28 cm long, 3.3–4.8 cm wide, broadest in lower third, sometimes erect, usually spreading to reflexed, often twisted and rolled up, inserted at 10°–30° angle on peduncle; spadix sessile, pale green (B & K Green 8/2.5), (3)7–18(28) cm long, 10–20 mm diam. at base, 6–12 mm diam. at apex; flowers 4-lobed, to 1.8 mm long, to 1.5 mm wide, the sides jaggedly sigmoid; 12–15 flowers visible in the principal spiral, 17–19 flowers visible in the alternate spiral; tepals semiglossy, the lateral tepals to 1 mm wide, the inner margin ± straight; pistils slightly emergent, very glossy, whitish green with darker green stigmatic area; the stigma elliptic, 0.2 mm long, glossy, exserted with glistening papillae; stamens emerging scattered throughout the spadix, sometimes with the alternate stamens preceding the lateral ones; filaments ca. 1 mm long, anthers pale yellow, ca. 4 mm long and 5–6 mm wide; thecae oblong; pollen yellow, fading white. INFRUCTESCENCE usually pendent, spathe often absent; spadix 15–40 cm long, to 2.5 cm diam.; berries ovate to ovate-elliptic, acute to rounded and green at apex, greenish-white to yellowish-green at base (white fide label of *Allen 2419*) to 9 mm long, ca. 5 mm wide; seeds 2, oblong and ± flattened, dark brown, 3.5–5 mm long, 2.2–2.4 mm wide, 1.5–1.8 mm thick. Figs. 24 and 25.

The species is known from Costa Rica and Panama and is to be expected in Colombia on the southwestern slopes of the Serranía de Pirre. It occurs on both the Atlantic and Pacific slopes. In Costa Rica, it ranges between 850 and 2,000 m but in Panama it has been collected as low as 400 m. The species inhabits premontane wet forest, premontane rain forest and lower montane rain forest.

Anthurium caperatum is recognized by its large, ovate leaves that have most of the veins of the upper surface sunken, giving the leaf a slightly bullate appearance, and a collective vein which arises from one of the lower pairs of basal veins. Other characteristic features include the green, brittle spathe, the pale green spadix, prominently exserted stamens, exserted pistils, greenish berries, and the dominance of pale green and yellowish pigments on all parts of the dried plant.

The species is similar to *Anthurium panamense* Croat (ined.), but that species has more elongate blades which are glossier on the upper surface, less protruded styles, weakly ribbed petioles, and red berries. The sectional placement of *A. caperatum* is as yet uncertain. It appears to be related to South American species in the *A. corrugatum* Sodiro complex. These were placed in section *Polyneurium* by Engler.

COSTA RICA. Border of PUNTARENAS & ALAJUELA: around Monteverde Nature Reserve, *Burger & Baker 9676* (F); *Dryer 423* (CR, F); *Utley & Utley 2419* (F). ALAJUELA: Catarata de San Ramón, *Brenes 13510* (F); stream near road from Cariblanco to Lake Hule about 2 km W of Hwy. 9, *Baker et al. 226* (F); woods along Río Aquilar on road to Lake Hule, *Lent 3255* (F). Cerro Carabove Zapote, *A. Smith 928* (F). CARTAGO: Cerro Carpintera, *Standley 35575, 35663* (US); near Copey, Cordillera de Talamanca, *Williams 16417* (EAP, F); near Moravia along road to Turrialba, *Burger & Ramirez 4015* (CR, F); Pacuare, Turrialba, *Ocampo 1431, 1433* (CR); below Palo Verde, *Luteyn 3330* (DUKE); near Río Tapemechin, *Lent 3734* (F); lower slopes of Alto Patillos, SE of Tapantí, *Lent 1082* (CR, F); forest above Río Grande de Orosi, S of Tapantí, *Lent 941* (F); Hwy. 32 to Limón, NE of Turrialba, *Croat 43358* (MO); S of Tapantí on E slope above the Río Grande de Orosi, *Burger & Stolze 5659* (CR, F); *Burger & Liesner 6855* (F); *Burger & Burger 7584* (MO), *7585* (F, NY); *Burger & Gentry 9203* (F); Tapantí Hydroelectric Reserve, *Croat 36069, 36211, 36216* (MO); road from Moravia to Quebrada Platanillo, *Croat 36616, 36679* (MO); Tapantí Watershed Preserve, SW of Paraíso, *Croat 47041* (MO). HEREDIA: 3 miles S of Cariblanco, *Croat 35832, 35835* (MO); above San Miguel, valley of Río Sarapiquí, *Moore 6580* (BH); E slopes of Volcán Barba between Río Las Vueltas and Río Nuevo, *Burger & Baker 9475* (F, MO); vicinity Río El Angel between Vara Blanca and Cariblanco, *Moore 6613* (BH); near Río Las Vueltas, NE of Volcán Barba, *Lent 2637* (CR, F); vicinity of Bajo La Hondura, *Croat 44518* (CR, F.

MO, US). HEREDIA & SAN JOSÉ: Cerro de Zurquí, *Burger & Baker 9323* (F). SAN JOSÉ: Valley of Río La Hondura, below La Palma, NE of San Jerónimo, *Burger & Stolze 4921* (CR, F); Bajo La Hondura, *Utley & Utley 4994* (DUKE); forest above Río La Hondura, *Lent 3784* (F); between San Isidro del General and Dominical, *Croat 35243, 35322* (MO).

Anthurium carnosum Croat & Baker, Brenesia 16 (Supl. 1): 36. 1979. TYPE: Costa Rica. San José and Cartago Provinces: along Inter-American Highway near Trinidad and Km 72 (about 20 km SE of El Empalme), cut over area, 2,600–2,800 m elevation; *Burger & Baker 9545* (F-1831851, holotype; MO-2385461, isotype).

Epiphytic vine, rarely terrestrial; stems slender, canelike, erect or trailing, to 1 m or more long, 5–7 mm diam., with thin, grayish, smooth periderm; internodes 2–9 cm long, shorter near apex; roots slender, elongate, frequently branching; cataphylls moderately thick, 2–6.5 cm long, with a subapical apiculum 2–3 mm long, encircling stem, persistent at upper nodes, drying thin, dark brown, deciduous except for a few pale, threadlike fibers. LEAVES with petioles 3–12 cm long, 2–3 mm diam., weakly sulcate; geniculum 1–2 cm long; blades coriaceous, succulent, lanceolate-elliptic, narrowly elliptic or sometimes oblanceolate-elliptic, gradually long-acuminate at apex, acute to attenuate at base, (7)9–15(17) cm long, (1.7)2.5–5(7) cm wide, broadest at or about the middle; both surfaces semiglossy, the lower surface slightly paler; midrib convexly raised above, diminished and sunken before the distal two thirds, raised throughout its length below; primary lateral veins 9–13(20) per side, departing midrib at 25°–50° angle, weakly sunken above, prominulous below, lesser veins inconspicuous above, prominulous below; collective vein arising from near the base, 2–7(12) mm from the margin, obscure to weakly sunken above, slightly raised below. INFLORESCENCE spreading, ± equalling leaves; peduncle 7–13 cm long, ca. 2 mm diam., ⅔ to 2 times longer than petioles; spathe thin, pale green, broadly lanceolate to oblong, 2.5–4.3 cm long, 8–14 mm wide, broadest in the lower third, acuminate at apex, obtuse to weakly lobed at base, inserted at ca. 45° angle on peduncle; stipe 5–8 mm long in front, 2–5 mm long in back, ca. 2 mm diam., green; spadix green, becoming yellowish and finally orange in fruit, (2.5)3–5.5 cm long, 3–4 mm diam. at base, 1.5–3 mm diam. at apex; flowers rhombic to 4-lobed, to 4 mm long, to 1.5 mm wide, the sides sigmoid; 1–2 flowers visible in the principal spiral, ca. 2 flowers visible in the alternate spiral; tepals dark green, the lateral tepals (1.5)2.5–3.5 mm wide, the inner margin convex; pistil emergent, green; stigma ellipsoid, ca. 0.3 mm long; stamens held just above tepals, the anthers yellowish-white, 0.3–0.5 mm long, 0.7–0.8 mm wide; thecae broadly ovate to suborbicular, weakly divaricate; pollen yellowish-white, drying white. INFRUCTESCENCE pendent, the spathe persisting; the spadix 6–10 cm long, 8–10 mm diam.; berries ovoid, acute at apex, yellow becoming bright orange, 9–11 mm long, 6–8 mm diam.; mesocarp thick, gelatinous, pale orange; seeds usually 2, sometimes 3 or 4, broadly ovate, rounded on both ends, flattened, ca. 3 mm long, 2 mm wide, 0.8 mm thick. Figs. 29 and 30.

Anthurium carnosum ranges from Costa Rica to Panama at elevations from (700)1,500 to 2,600(3,000) m. It inhabits premontane rain forest, lower montane wet forest, lower montane, and montane rain forest life zone formations. In Costa Rica it is known from the Cordillera Central, Volcán Turrialba, as well as on the western end of the Cordillera de Talamanca in the vicinity of Tapantí and Cerro de la Muerte, but it is to be expected throughout the Talamanca range to Panama. The species is common at 2,400 to 2,600 m elevation on Cerro de la Muerte and shares this habitat with only one other aroid, the cordate-leaved *Anthurium concinnatum* Schott. In Panama, the species has been found more widely, being known from a number of localities in Chiriquí Province.

Anthurium carnosum is recognized by its scandent habit, its thick, succulent leaves with strongly discolorous surfaces, and its usual montane habitat. It is closely related to *A. flavescens* Poepp. of Peru, but differs from that species in fewer lateral veins, a shorter peduncle, dark green tepals (white for *A. flavescens*), and a longer, thinner spadix. Among Central American species, *A. carnosum* is most closely related to *A. pittieri* Engler and *A. interruptum* Sodiro. *Anthurium carnosum* differs from *A. pittieri* by its longer internodes, viney habit, non-decurrent spathe, and its thick, succulent leaves. No intermediates have been found and they do not appear to be variants of one another. *Anthurium carnosum* differs from *A. interruptum* in its higher altitu-

FIGURES 30–33. 30. *Anthurium carnosum* Croat & Baker, *Croat 48619*.—31–32. *Anthurium cerrobaulense* Matuda, *Croat 47640*.—33. *Anthurium chamulense* ssp. *oaxacanum* Croat, *Croat 48389* (Type).

dinal range, short-stipitate spadix, orange (vs. red) berry color, shorter internode length, and thicker leaves. The sectional placement of *A. carnosum* is uncertain but it has been tentatively placed in section *Xialophyllium.*

COSTA RICA. No other location, *O. Jiménez 29* (US). Probably CARTAGO or SAN JOSÉ: El Páramo, *Pittier 10534* (CR). CARTAGO: S of Cartago, Cordillera de Talamanca, *Williams et al. 28115* (EAP, F); *28247* (F); slopes of Volcán Turrialba, *Utley 151* (DUKE); Cerro del Roble (Copey), *Tonduz 11829* (CR); Trinidad, SE of El Empalme, *M. Jiménez 2199* (CR, F); NW slope of Cerro de la Muerta along Interamerican Hwy. *Croat 35416* (MO); S of Tapantí above Río Grande de Orosi, *Burger & Liesner 6724b* (F); SE of El Empalme on the Interamerican Hwy. *Utley & Utley 856, 1698* (CR, F). CARTAGO & SAN JOSÉ: SE of El Empalme along the Interamerican Hwy. *Burger 7978* (CR, F); near Trinidad, along the Interamerican Hwy. *Burger & Stolze 5227* (CR, F); *Burger & Baker 9545* (F, MO). SAN JOSÉ: N of Santa María de Dota, *Standley 43087, 43096, 43100* (US); near Finca La Cima, N of Copey, *Standley 42635, 42682, 42726, 42732, 42747* (US); Lake Chonta, NE of Santa María de Dota, *Standley 42161, 42307, 42313, 42364* (US); near Lake La Escuadra, NE of Copey, *Standley 41956, 41990, 42060, 42061* (US); near Río Parrita Chiquita, N of Santa María de Dota, *Lent 3911* (CR, F).

Anthurium cerrobaulense Matuda, Anales Inst. Biol. Univ. Nac. México 30: 112–113. 1960. TYPE: Mexico. Oaxaca: Cerro Baúl (on the border of Oaxaca and Chiapas NW of Rizo de Oro located on Hwy. 190), November 15, 1957, *MacDougall 276* (MEXU, holotype).

Epiphyte or on rocks, rarely terrestrial 17–40 m tall; stems 2.5–4 cm diam.; leaf scars 1–2 cm wide; roots 4–5 mm diam., tan, descending; cataphylls 2–5 cm long, green tinged with red-violet, rounded at apex with a subapical apiculum extending beyond the apex ca. 3 mm, drying medium brown and weathering into fibers. LEAVES erect-spreading; petiole 15–45 cm long, 3–6 mm diam., broadly and sharply sulcate adaxially, rounded abaxially (sometimes tinged with red-violet); geniculum 1–1.7 cm long; blades ovate to triangular (when flattened), often with midrib arching upward, thick, acute at apex, broadly lobed at base, (10)23–37 cm long, 13–18.5 cm wide, broadest at point of attachment or just below (often broader at base when flattened); anterior lobe 14–25.5 cm long, the margins convex at base becoming straight or markedly concave; posterior lobes 7–13 cm long, directed upward at almost 90° angle or directed outward when flattened, the upper surface glossy, lower surface semiglossy; midrib convexly raised to midway, then sunken to apex, sharply raised nearly to apex below, then sunken; basal veins 3–5 pairs, the first free to base, the third to fifth coalesced 4–5 cm, raised and darker than surface above and below, the posterior rib naked, the outer margin rolled up; primary lateral veins 5–9 per side, departing the midrib at 45° angle, sunken above, prominulous and darker than surface below; interprimary veins sunken, lesser veins scarcely visible; collective vein arising from the first basal vein, sometimes loop-connected with the third or fourth basal vein, 0.5–1.5 cm from margin, sunken above, raised below. INFLORESCENCE erect-spreading; peduncle 22–40 cm long, 4–5 mm diam., terete, pale green; spathe relatively thin, green sometimes tinged with violet, lanceolate, 2.3–5 cm long, 1.2–1.7 cm wide, broadest just above the base, abruptly acuminate at apex, inserted at 45° angle on peduncle; the stipe 6 mm long in front, 2 mm long in back, pale green sometimes tinged with red at base of spadix; spadix green, heavily tinged red-violet along inner edges of tepals, 4–4.4 cm long, 7–8 mm diam. at base, 4–5 mm diam. at apex; the flowers 4-lobed, ca. 3 mm long, 3.5 mm wide, the sides sigmoid; 5–8 flowers visible per principal spiral, 3–6 flowers visible in the alternate spiral; tepals matte, with copious droplets when stamens are emerging; lateral tepals 1.2–1.5 mm wide, the inner margin turned up; pistil slightly emergent, purple; stigma a shallow depression; stamens developing from the base, the laterals followed by the alternates in rapid succession, with the leading spirals preceding the alternates by 1 or 2 spirals; stamens held above pistil on transparent filaments 0.4–0.6 mm long, 0.6–0.9 mm wide, then retracting to edge of tepals before next one appears; anthers pale yellow; thecae ± oblong, somewhat divaricate; pollen cream, soon dispersing. INFRUCTESCENCE spreading-pendent; spathe persisting; spadix 9.5–12 cm long, 2.3 cm diam.; immature berries emergent ca. 4 mm, dull violet-purple; mature berries red, to red-orange, obovoid, mammilliform at apex, 1.5–1.6 cm long, 1–1.7 cm wide, mesocarp thickly gelatinous to mealy with numerous short raphide cells; seeds 1–2, obovoid, green to yellow-green, 9–10 mm long, 7.6–8 mm wide, flattened, with a flattened truncate gelatinous appendage at the base. Figs. 31, 32, and 34.

Anthurium cerrobaulense is restricted to Mexico in the SW corner of Chiapas in the Munici-

FIGURES 34–37. 34. *Anthurium cerrobaulense* Matuda, *Croat 47640*.—35–37. *Anthurium cerropelonense* Matuda, *Croat 48180*.

pios of Cintalapa and Arriaga at elevations of 830 to 1,600 m in "bosque pino-Encino."

The species is tentatively placed in section *Belolonchium* and is distinguished by its thick leaf blades with usually prominent, elongate, narrow posterior lobes that are directed usually upward at an angle of 45° to 90° to the midrib, and also by its relatively much paler lower blade surface with only obscurely visible tertiary veins.

Anthurium cerrobaulense is most easily confused with *A. chamulense,* which has leaves of similar coloration and texture, but that species is distinguished by having the blades merely subcordate or by having the posterior lobes merely rounded.

MEXICO. CHIAPAS: north of Arriaga, *Breedlove & Thorne 30579* (DS); vicinity Cerro Baúl, *Breedlove 21695, 24716, 31356* (DS); *Croat 47640* (MO); east of San Pedro Tapanatepec, *Breedlove 9975* (DS).

Anthurium cerropelonense Matuda, Bol. Soc. Bot. México 24: 37. 1959. TYPE: Mexico. Oaxaca: road between Cerro Pelón and Yetla, 2,600 m, *MacDougall 405* (MEXU).

Epiphyte or on rocks; to ca. 1 m tall; stems 4–8 cm diam.; leaf scars 4–6 cm wide; roots thick, tan, descending; cataphylls coriaceous 9–13 cm long, acuminate at apex, subapical apiculum 1 cm long, drying dark brown, persisting intact at apex, splitting at base into coarse fibers. LEAVES erect to spreading; petioles 27–78 cm long, 5–17 mm diam., subterete, weakly sulcate; geniculum 2–3 cm long; blades subcoriaceous, ovate, acute at apex (the acumen minutely apiculate), deeply lobed at base, 30–65 cm long, 20–50 cm wide, broadest near point of petiole attachment, the margins somewhat irregular and undulate; anterior lobe 23–50 cm long, the margins convex; posterior lobes 7–20 cm long directed upward or flat; the sinus spathulate, acute at apex; both surfaces matte to semiglossy; midrib convexly raised above and below, diminishing and sunken at apex above; basal veins 8 pairs, the first and second (sometimes third) free, up to 5 coalesced 1–2 cm, raised above and below; posterior ribs not marginal; leaf tissue turned up at margins; primary lateral veins 5–7 per side, departing midrib at 35° angle, sunken above, raised below, arcuate-ascending, loop-connected near the apex; lesser veins conspicuous and flat on upper surface, prominulous on lower surface; collective vein arising from first basal vein or one of the uppermost primary lateral veins, 10–18 mm from margin, sunken above, raised below. INFLORESCENCE spreading, shorter than leaves; peduncle 22–45 cm long, 8 mm diam., terete, ½–⅔ as long as petioles; spathe subcoriaceous, medium green (B & K Yellow-green 6/7.5), tinged at margins with purple or very heavily tinged with purple inside, narrowly ovate, 9.5 cm long, 2.3–4 cm wide, broadest near base, caudate-acuminate at apex (the acumen ca. 1 cm long), obtuse to rounded at base and clasping, inserted at 30° angle on peduncle; spadix violet-purple, sometimes green turning violet-purple (B & K Red-purple 2/5), 5–11 cm long, 0.8–1.5 cm diam. at base, 5–7 mm diam. at apex; flowers square, 2.7–3 mm in both directions, the sides weakly sigmoid; 10–14 flowers visible in the principal spiral, 8–12 flowers visible in the alternate spiral; tepals matte, with dense, pale punctations, minutely papillate; lateral tepals 1.8–2.2 mm wide, the inner margin convex; pistil not visible before anthesis; stamens developing from the base in a complete sequence, the leading lateral stamens 1–2 spirals ahead of the fourth stamen; anthers ca. 1.2 mm long, 0.5 mm wide; thecae ovate-oblong, scarcely divaricate. INFRUCTESCENCE pendent; spadix to 15 cm long, 4 cm diam.; berries obovoid, mammilliform at apex, orange (?), 9–10 mm long, 7–9 mm diam.; mesocarp fleshy, thick; seeds usually 2, 7 mm long, 4.5–5.5 mm wide. Figs. 35, 36, and 37.

Anthurium cerropelonense is endemic to the Sierra de Juárez in the Sierra Madre Oriental in Oaxaca at 2,400 to 2,800 m in cloud forests near the summit of the Atlantic slope. The forest type is "selva alta perennifolia." All collections have been made along Highway 175.

The species is characterized by its large, thick, ovate-cordate blades, narrow or closed sinus, posterior rib rather distant from the leaf margin, and by conspicuous tertiary veins, and also by its thick, dark violet-purple spadix.

Unlike most Mexican species, which appear to be related to several other species, *A. cerropelonense* seems to be unrelated to or confused with any other species. It is tentatively placed in section *Belolonchium.*

MEXICO. OAXACA: between Cerro Pelón & Yetla, *MacDougall 405* (MEXU); vicinity of Ixtlán de Juárez, *Almeda & Luteyn 1666* (DUKE); *Graham & Frohlich 1105* (MICH); between Tuxtepec & Oaxaca, *Croat 48180* (MO).

Anthurium chamulense Matuda, Anales Inst. Biol. Univ. Nac. México 27: 339. Fig. 2. 1957.

a. Anthurium chamulense ssp. **chamulense.** TYPE: Mexico. Chiapas: San Juan Chamula (just NW of San Cristóbal de Las Casas) *MacDougall 348* (MEXU, holotype—not found).

Anthurium motozintlense Matuda, Anales Inst. Biol. Univ. Nac. México 43, Ser. Bot. (1): 55. Fig. 4. 1972 (Publ. 1974). TYPE: Mexico. Chiapas: Sierra Madre, El Rosario, Motozintla, 1,800 m elev. *MacDougall 393A* (MEXU, holotype).

Anthurium monserratense Matuda, Anales Inst. Biol. Univ. Nac. México 27: 342. Fig. 3. 1957. TYPE: Mexico. Chiapas: Municipio of Cintalapa, near Finca Monserrate, alt. 1,000 m. *MacDougall 285* (MEXU, not seen).

Epiphyte or on rocks; roots tan (dry), ca. 2 mm diam.; cataphylls subcoriaceous, 3.5–10 cm long, rounded at apex (subapical apiculum ca. 2 mm long), drying medium to dark brown (B & K Yellow-red 4/10), persisting as reticulate fibers. LEAVES usually erect; petioles D-shaped, 14–32(47) cm long, 2–6 mm diam., sharply and broadly sulcate; geniculum 1.5–2 cm long; blades coriaceous, narrowly to broadly triangular, 13–37 cm long, 5–26.5 cm wide, broadest 1–2 cm above base, acute to narrowly rounded and apiculate at apex (the apiculum 1–2 mm long), truncate to obtuse or broadly lobed at base; anterior lobe 13.5–30 cm long; posterior lobes 3.2–12 cm long; sinus arcuate to arcuate with decurrent petiole, rounded at apex; upper surface semiglossy, the lower surface matte to semiglossy; midrib bluntly raised at base, diminished and sunken at apex above, raised at base, flat at apex below; basal veins 3–5, the uppermost free (sometimes all free), third or fourth coalesced to 3.5 cm; posterior rib naked, turned up; primary lateral veins 7–19 per side, departing midrib at 45° angle, sunken but scarcely more conspicuous than lesser veins above, prominulous and darker than surface below; submarginal collective vein arising from first or second basal veins; third basal vein loop-connected to collective vein, 2–15 mm from margin. INFLORESCENCES erect to spreading, shorter than or as long as the leaves; peduncle 27–48 cm long, 3 mm diam.; spathe moderately thin, pale green tinged pink at base and apex, ovate to ovate-lanceolate, 3.5–14 cm long, 1.3–6 cm wide, broadest just above base, abruptly to gradually acuminate at apex, rounded to truncate at base, inserted at 10° angle on peduncle, the area around stipe thickened, donut-shaped; stipe 3 mm long in front, 1.5 mm long in back, green; spadix green becoming slightly to heavily tinged with violet-purple (B & K Red-purple 2/5), 3–13 cm long, 5.5–10 mm diam. at base, 3–6 mm at apex; the flowers rhombic, 2.2–2.3 mm long, 2.4–2.5 mm wide, the sides straight to broadly sigmoid; 5–6 flowers visible in the principal spiral, ca. 5 flowers visible in the alternate spiral; tepals matte, sparsely punctate, minutely papillate, lateral tepals 1.6 mm wide, the inner margins broadly rounded; pistil emergent, bright green; stigma a nearly obscure slit; stamens emerging in a prompt and complete sequence beginning at base, sometimes with as many as 3 emerging simultaneously, the leading stamens no more than 3 spirals ahead of completed sequence; anthers cream-colored, held in a tight cluster obscuring pistil, 0.8 mm long, 0.9 mm wide, shrinking to 0.4 mm wide; thecae ovate, slightly divaricate; pollen white. INFRUCTESCENCE pendent, 7–10 cm long, 1.5 cm diam.; spathe persistent, berries red, obovate to round; seeds not seen. Fig. 38.

The species is known only from southern Mexico in Oaxaca and Chiapas and consists of two subspecies. Subspecies *oaxacanum* Croat is known only from the type locality in northwest Oaxaca in "selva alta perennifolia," while subspecies *chamulense* is widespread in Chiapas and is expected also in Guatemala. It ranges from 1,500 to 3,000 m and is perhaps restricted to regions of "bosque pino-encino." Most collections have been made from northern Chiapas but the species has also been collected in the Municipio of Motozintla in southeast Chiapas and also in the Municipio Villa Corzo in south central Chiapas. One of the collections from the latter collecting area (*MacDougall 376*) is somewhat aberrant in that it has a thicker blade with more conspicuous posterior lobes. This specimen perhaps represents a distinct species but it is too incomplete to be certain.

Anthurium chamulense is tentatively placed in section *Belolonchium* and is distinguished by its coriaceous, ovate-triangular leaf blade usually with short lobes and broad sinus (when flattened). Live plants (especially those populations seen at Pueblo Nuevo Solistahuacán) exhibit a characteristic vein pattern with the tertiary veins scarcely visible on the lower surface but clearly visible and minutely etched on the upper surface.

FIGURES 38–41. 38. *Anthurium chamulense* Matuda, *Croat 46426*.—39. *Anthurium chamulense* ssp. *oaxacanum* Croat, *Croat 48389* (Type).—40–41. *Anthurium chiapasense* Standl., *Croat 40900*.

The species is probably closest to *A. andicola*, but that species can be distinguished by having usually conspicuous tertiary veins on the surface that are weakly elevated and darker than the surface. *Anthurium chamulense* is also very similar to *A. cerrobaulense* from southwest Chiapas because they both have leaves with similar coloration and texture, but that species has blades with usually conspicuous narrow, rather elongate, posterior lobes.

The type of *Anthurium monserratense* Matuda was not seen but the description, illustration, and the location of the collection make it rather conclusively synonymous with *A. chamulense*.

MEXICO. CHIAPAS: NE of Bochil, *Breedlove 34643* (DS); Cerro Tres Picos, *Breedlove 24972, 30125* (DS); *MacDougall 376* (MEXU); El Rosario, *MacDougall 393A* (MEXU); *Matuda 37603* (DS, MEXU); near Ocosingo, *Breedlove 16021, 16033, 16034* (DS); Pueblo Nuevo Solistahuacán, *Croat 46426, 47765* (MO); *Luteyn & Almeda 3443* (DUKE); *Mill 220, 595, 673* (DS); *Raven & Breedlove 20034* (DS, ENCB); *Roe et al. 1239* (US); *Thorne & Lathrop 40392* (DS); Tenejapa, *Breedlove & Raven 12916* (DS); vicinity Tuxtla Guttiérrez, *Clarke 175* (DS); Munc. Zinacantán, *Laughlin 536* (DS, DUKE, ENCB).

b. Anthurium chamulense ssp. **oaxacanum** Croat, ssp. nov. TYPE: Mexico. Oaxaca: along road from Teotitlán del Camino to Santa María Chilchotla, 4.4 mi beyond turnoff to Huatla de Jiménez, elev. 1,980 m, steep slopes with huge boulders, *Croat 48389* (MO-2682519, holotype; F, K, MEXU, SEL, US, isotypes; Live at MO).

Anthurium chamulense ssp. *oaxacanum* a ssp. *chamulense* laminis tenuioribus, nervis tertiaribus supra vix impressis subtus manifestis differt.

Epiphyte; stems narrow, 1.5 cm diam.; leaf scars 1.2 cm wide; roots thick, brown; cataphylls subcoriaceous, 4–7 cm long, drying medium brown (B & K Yellow 4/10), persisting as reticulate fibers. LEAVES erect-spreading; petioles 22–30 cm long, 4–6 mm diam., D-shaped, bluntly sulcate, the margins sharper near base of blade; geniculum 1–1.3 cm long, sometimes tinged red-violet; blades subcoriaceous, triangular, 24–48 cm long, 8–13 cm wide, broadest 1–2 cm from base, gradually acuminate at apex, obtuse to truncate at base; anterior lobe 23.5–27 cm long, the margins straight; posterior lobes 4–5.5 cm long, directed upward; sinus arcuate to arcuate with petiole decurrent, rounded at apex; upper surface glossy, lower surface matte; midrib bluntly raised at base, sunken to flat at apex above, raised below; basal veins 3–4 pairs, the second to fourth coalesced 1–1.5 cm, prominulous above and below; posterior ribs naked, the outer margins rolled up; primary lateral veins 3–6 per side, departing midrib at 30°–45° angle, sunken above, raised below, straight to collective vein; lesser veins scarcely visible; collective vein arising from the first or second basal vein, running to the apex, 3–5 mm from margin, sunken above, raised below. INFLORESCENCE spreading, shorter or as long as leaves; peduncle terete, green, tinged with red-violet, 30–32 cm long, 3–4 mm diam.; spathe green, subcoriaceous, ± triangular, ca. 3 cm long, 1 cm wide; spadix violet-purple, tan at anthesis, 4.5–5 cm long, 5–6 mm diam. at base, 3–4 mm diam. at apex; flowers rhombic, 3 mm in both directions, the sides straight to weakly sigmoid; 3–6 flowers visible in the principal spiral, 4–8 flowers visible in the alternate spiral; tepals matte, weakly punctate, minutely papillate, lateral tepals ca. 1.5 mm wide, the inner margin convex; pistils weakly emergent; stigma linear; stamens emerging from base, laterals first, preceding alternates by 3–4 spirals, held over pistil in tight cluster; anthers white; thecae ellipsoid, not divaricate; pollen white to cream. INFRUCTESCENCE pendent; berries pale orange, truncate at apex, trapezoidal in side view, ca. 10 mm long, 8–11 mm diam.; mesocarp juicy, fleshy with numerous, whitish raphide cells; seeds 2, greenish white, obovate, depressed at apex, round at base, flattened, ca. 7 mm long, 6 mm wide, 3.1–3.4 mm thick, enveloped in a thin, sticky substance, slightly longer on ends than at sides of seeds. Figs. 33 and 39.

Anthurium chamulense ssp. *oaxacanum* is known only from the type locality in northern Oaxaca in "selva alta perennifolia" at nearly 2,000 m. The taxon is recognized by its relatively thinner, usually truncate, narrowly triangular leaves, sulcate petiole, green spathe and short, usually stipitate, violet-purple spadix. It is a member of section *Belolonchium*.

The subspecies *oaxacanum* is not confused with any other taxon from that part of Mexico. It is separated from *A. chamulense* ssp. *chamulense* by having thinner leaf blades with less conspicuously impressed tertiary veins on the upper surface but with the tertiary veins on the lower surface clearly visible. In subspecies *chamulense* the tertiary veins on the lower surface

are scarcely visible. In addition the subspecies *oaxacanum* occurs in much wetter forest ("selva alta perennifolia") than ssp. *chamulense* ("bosque pino-encino").

MEXICO. OAXACA: between Teotitlán and Santa María Chilchotla, beyond turnoff to Huatla de Jiménez, *Croat 48389* (F, K, MEXU, MO, SEL, US).

Anthurium chiapasense Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 67. 1940.

a. **Anthurium chiapasense** ssp. **chiapasense.** TYPE: Mexico. Chiapas: Monte Ovando (just NW of Escuintla) *Matuda 1562* (MO, holotype).

Anthurium cuspidatum Matuda, Madroño 10: 169. 1950, non Mast., 1875. *Anthurium cruxiphyllum* Matuda, Revista Soc. Mex. Hist. Nat. 11: 93. 1950. TYPE: Mexico. Chiapas: near Colonia Jalapa, 32 km E of Escuintla, elev. 700 m, *Matuda 18316* (MEXU, holotype; F, isotype).

Epiphyte; stems 2–4 cm long, 2.5 cm diam.; internodes and leaf scars obscured by cataphylls; roots moderately thick, green, descending; cataphylls subcoriaceous, 3–6 cm long, acute at apex (apiculate to 2 mm), drying brown (B & K Yellow 3/10), weathering to reticulate fibers and persisting. LEAVES erect-spreading; petioles 10–51 cm long, 3–6 mm diam., terete; geniculum 1.7–2 cm long, sometimes shallowly sulcate; blades moderately thick, narrowly triangular, long acuminate at apex, broadly lobed at base, 13–42 cm long, 5.5–25 cm wide, broadest at base; anterior lobe 11.5–36 cm long, the margins ± straight; posterior lobes 2.5–10.5 cm long; sinus arcuate, round at apex; both surfaces matte, lower surface densely glandular-punctate; midrib acutely raised at base above, flat at middle, sunken at apex, acutely raised throughout below; basal veins 3–4 pairs, the third and fourth coalesced 1.5–2 cm, flat to weakly sunken above, raised below; the posterior rib naked, the outer margin turned up; primary lateral veins 2–3 per side, departing midrib at 30° angle, weakly sunken, nearly obscure above, prominulous below, ± straight to collective vein, lesser veins obscure; collective vein arising from the uppermost basal vein, 0.7–1.5 mm from margin, sunken above, raised below. INFLORESCENCE erect-spreading; as long as or longer than leaves; petiole 30–57 cm long, 2.5–4 cm diam., terete; spathe green, tinged with violet-purple, lanceolate; 4.5–7 cm long, 1–1.8 cm wide, cuspidate-acuminate at apex, rounded at base, broadest just above base, inserted at 50° angle on peduncle; spadix deep purple (B & K Red-purple 2/2.5), 7.4–10.5 cm long, 5.5–8 mm diam. at base, 3–4 mm diam. at apex, the flowers square to sub-4-lobed, 2.3–2.5 mm in both directions, the sides straight to jaggedly sigmoid; 4–7 flowers visible in the principal spiral, 7–8 flowers visible in the alternate spiral; tepals matte to weakly glossy, obscurely punctate, minutely papillate; lateral tepals 1.2–1.5 mm wide, the inner margins broadly rounded; pistils raised, not emergent until just before stamens emerge, green tinged with purple, weakly papillate; stigma linear, ca. 0.3 mm long, scarcely distinguishable; stamens emerging from base, lateral stamens emerging to midway, before alternates emerge at base; anthers yellow, 0.5 mm long, 0.6 mm wide, held just above tepals; thecae oblong-elliptic, slightly divaricate; pollen yellow, fading cream. INFRUCTESCENCE not known. Figs. 40 and 41.

The species consists of two subspecies. *Anthurium chiapasense* ssp. *chiapasense* occurs in Mexico in southeastern Chiapas and southwestern Guatemala at elevations of 800 to 1,900 m. The type locality is probably tropical wet forest and is mapped as "bosque de oyamel" (Flores et al., 1971) on the Mexican vegetation map, but the species also occurs in "bosque cauducifolio" and "bosque pino-encino." Subspecies *tlaxiacense* (Matuda) Croat is endemic to southern Oaxaca and differs from the typical subspecies in having an olive green spadix at anthesis and blades with the primary lateral veins prominently raised on the lower surface.

Anthurium chiapasense is in section *Belolonchium* and is characterized by its thick blades that are much paler and conspicuously punctate on the lower surface with an oblong or narrowly triangular anterior lobe, 3–9 cm wide midway.

The species is closely related to *A. lucens* and may prove to be only subspecifically distinct from that species. Although both species share a relatively short, dark violet-purple spadix, subcoriaceous, glandular-punctate leaf blades, and bright red berries, *A. chiapasense* differs from *A. lucens* in having slender anterior lobes with concave margins. The margins of the anterior lobe of *A. lucens* are generally conspicuously convex.

Anthurium chiapasense has a leaf shape more similar to that of *A. verapazense*, which also has subcoriaceous, glandular-punctate leaves. It differs from *A. verapazense* in having a porportionally much shorter spadix with the spathe more than half as long as the spadix at anthesis. In

addition, *A. verapazense* occurs from sea level to less than 1,000 meters, whereas *A. chiapasense* occurs from 800 to 1,800 m. Typical *A. verapazense* has a long, slender spadix well over twice as long as the spathe at anthesis.

Anthurium chiapasense differs from both *A. lucens* and *A. verapazense* in usually drying blackened while the other two species usually dry greenish to greenish-brown. It is tentatively placed in section *Belolonchium*.

GUATEMALA. SAN MARCOS: Finca Armenia above San Rafael, *Croat 40900* (MO).

MEXICO. CHIAPAS: Escuintla, *Matuda 18315* (DS, MEXU, UCLA); *Matuda 18443* (CAS, MEXU, NY); *Matuda 18159A, 18159, 18316, 18363, 18491* (MEXU); *Matuda 18573* (CAS, DS, MEXU); *Matuda 18629* (MEXU, NY); Montebello, SE of Comitán, *Carlson s.n.* (MEXU); Monte Ovando, *Matuda 1562* (MEXU, MICH, MO); *Matuda 17930* (MEXU); Motozintla, *Breedlove & Thorne 31026* (CAS, DS); Porvenir, *Matuda 30186* (MEXU). MÉXICO: San Angel, *De la Cerda 81* (MEXU).

b. Anthurium chiapasense ssp. tlaxiacense (Matuda) Croat, comb. nov. *Anthurium tlaxiacense* Matuda, Anales Inst. Biol. Univ. Nac. México 32: 149, Fig. 6. 1961. TYPE: Mexico. Oaxaca: Cerro de la Virgin, Tlaxiaco (just E of Tlaxiaco); elev. 1,500 m. *MacDougall s.n.* (MEXU, holotype).

Epiphytic or epipetric; stems to 6 cm long, 2 cm diam.; internodes and leaf scars obscured by cataphylls; roots moderately thick, green; cataphylls subcoriaceous, 6.7–8 cm long, acute at apex (apiculate to 1 mm), drying brown (B & K Yellow 4/5), weathering into coarse fibers, persisting around stem. LEAVES erect-spreading; petioles 37–64 cm long, 6–8 mm diam., ± terete; geniculum 2.5–4 cm long, sometimes weakly sulcate; blades subcoriaceous, narrowly triangular, 35–56 cm long, 13–30 cm wide, acuminate at apex (apiculate 5 mm), deeply lobed at base, broadest at base; anterior lobe 28–45 cm long, the margins round to convex; posterior lobes 9–12 cm long, directed upward; sinus hippocrepiform, acute at apex; upper surface matte to semiglossy, lower surface matte, glandular-punctate; midrib flat to convexly raised above, weakly sunken at apex, prominently raised below; basal veins 4–5 pairs, the third to fifth coalesced 1.5 cm, flat to weakly sunken above, raised below; posterior rib naked, turned up; primary lateral veins 5–6 per side, departing midrib at 20°–25° angle, sunken above, raised below, straight to collective vein; lesser veins obscure above, prominulous below; submarginal collective vein usually arising from the uppermost basal vein, 7–9 mm from the margin, sunken above, raised below. INFLORESCENCE spreading-pendent, equalling leaves; peduncle 53–57 cm long, 5–7 mm diam., terete; spathe subcoriaceous, yellow-green (B & K Yellow-green 7/5), lanceolate, 6–7 cm long, 1.5–1.7 cm wide, margins thin, transparent, soon withering, inserted at 40° angle on peduncle; spadix dark yellow-green to gray-green, heavily tinged red-violet at outer margins of tepals, 5.5–8.5 cm long, 6–9 mm diam. at base, 3–5 mm diam. at apex; the flowers 4-lobed, 2.3–3 mm long, 2.4–2.8 mm wide, the sides sigmoid; 6–8 flowers visible in the principal spiral, 6–7 flowers visible in the alternate spiral; tepals matte, weakly punctate, densely papillate, lateral tepals 1.3–1.6 mm wide, the inner margin convex; pistil raised, green, glossy; stigma elliptic, 0.4–0.5 mm long, deep purple with large globose droplet ca. 1 week before stamens emerge; stamens emerging from base, lateral stamens emerging throughout, alternates following within a few days, exserted well over pistil on fleshy, red-violet tinged filaments, retracting when anthers open; filaments ca. 5 mm long, ca. 6 mm wide, anthers pale yellow, ca. 0.6 mm long, 1.9 mm wide; thecae oblong, scarcely divaricate; pollen yellow fading cream. INFRUCTESCENCE arching-pendent; spathe usually absent; spadix 10–12(20) cm long, 1.5–3.5 cm diam. (5–6 cm diam. with berries fully emerged); berries ± obovoid to oblong-elliptic, rounded at apex, bright red (B & K Red 4/5); mesocarp translucent, juicy, with numerous raphide cells; seeds 1–2, green, streaked with purple, weakly flattened, 4.5–5 mm long, ca. 3 mm wide, 1 mm thick, enveloped in a transparent, amber, gelatinous sack. Figs. 42, 43, and 46.

Anthurium chiapasense ssp. *tlaxiacense* is endemic to southern Oaxaca and has been collected at 1,400 to 1,500 m in seasonally dry forest.

Anthurium chiapasense ssp. *tlaxiacense* is distinguished from ssp. *chiapasense* by its olive green spadix at anthesis and blades with the primary lateral veins prominently raised on the lower surface. It is recognized by its coriaceous, narrowly triangular-hastate leaf blade, dark green above and much paler and conspicuously glandular-punctate beneath.

MEXICO. OAXACA: between Pinotepa Nacional and Tlaxiaco, *Croat 45927* (MO); S of Miahuatlán on road between Oaxaca and Pochutla, *Croat 46126* (MO); Tlaxiaco, *MacDougall s.n.* (MEXU).

FIGURES 42–45. 42–43. *Anthurium chiapasense* ssp. *tlaxiacense* (Matuda) Croat, *Croat 46126*.—44. *Anthurium clarinervium* Matuda, *Selby 9-75-59*.—45. *Anthurium clarinervium* Matuda, *Croat 40646*.

FIGURES 46–49. 46. *Anthurium chiapasense* ssp. *tlaxiacense* (Matuda) Croat, *Croat 46126*.—47–48. *Anthurium clavatum* Croat & Baker, *Croat 36079* (Type).—49. *Anthurium clavigerum* Poepp., *Croat s.n.*

Anthurium clarinervium Matuda, Anales Inst. Biol. Univ. Nac. México 25: 203. 1954. TYPE: Mexico. Chiapas: NE of Ocozocoautla (collected by Ing. Ramirez August 5, 1951) *Matuda 25894* (MEXU, holotype).

Terrestrial, deeply rooted among rocks, less frequently epipetric in thin soil on rocks; stems 1–2 cm diam.; leaf scars 1.7 cm wide; cataphylls subcoriaceous, 3–4 cm long, obtuse at apex with subapical apiculum, pale red-violet with pale green speckles, drying brown (B & K Yellow 5/2.5), splitting and persisting. LEAVES erect to spreading; petioles 7–16 cm long, 4–6 mm diam., terete, green or pale red-violet with green speckles; geniculum 1–1.5 cm long; blades ovate, moderately coriaceous, abruptly to gradually acuminate at apex, deeply lobed at base, 11–25.5 cm long, 6.5–17 cm wide, broadest at middle or just below, the margin flat, drying conspicuously undulate; anterior lobe 6.5–18 cm long, the margins convex; posterior lobes 2.5–9 cm long; sinus spathulate to obovate, the lobes sometimes overlapping, acute at apex; upper surface matte, velvety, dark green, lower surface paler, matte; midrib convexly raised, diminishing at apex above, raised below; primary lateral veins 3–5 per side, raised above, flat below; interprimary veins conspicuous; basal veins 4–5 pairs, free to base or sometimes the third to fourth veins coalesced, the first curving to apex, the second to fourth arcuate-ascending to margin, loop-connecting; collective vein arising from first basal vein; all veins clearly outlined by white or greenish white area. INFLORESCENCE erect-spreading, longer than leaves; peduncles 16–38 cm long, 2–4 mm diam., terete, green tinged with red-violet, longer than petioles; spathe chartaceous, pale green tinged with violet-purple near margins (B & K Yellow-green 6/7.5), lanceolate, 3.7–6.5 cm long, 1–1.5 cm wide, broadest at base, narrowly acuminate at apex, obtuse at base, inserted at 40°–70° angle on peduncle; stipe to 5 mm long in front, to 2 mm long in back; spadix green, tinged with violet-purple sometimes appearing brown (B & K Yellow-green 5/5 to Yellow 4/10), 4.7–7.5 cm long, 4–7 mm diam. at base, 3–3.5 mm diam. at apex; flowers sub-4-lobed to square, 3.8–5 mm long, 3.2–5 mm wide, the sides jaggedly sigmoid; 3–4 flowers visible in the principal spiral, 5–8 flowers visible in the alternate spiral; tepals matte, papillate, densely and conspicuously punctate, large droplets visible as stamens emerge, lateral tepals 2.8–3.1 mm wide, the inner margin weakly concave; the pistils weakly emergent usually as soon as spathe opens, green; stigma elliptic, 0.6–1 mm long, brushlike, exserted with large droplets 2–3 days before stamens emerge; stamens emerging rapidly from base on flattened, translucent filaments 1 mm long, 1.5 mm wide, lateral stamens emergent to midway before alternates appear, retracting and held just above tepals; anthers yellow, 0.4–0.8 mm long, 0.7–1.5 mm wide, thecae elliptic, not divaricate, pollen cream fading to white. INFRUCTESCENCE with bright orange, subglobose berries, ca. 1.5 mm long; mesocarp mealy, seeds not seen. Figs. 44 and 45.

Anthurium clarinervium is probably endemic to Mexico, known only from areas with limestone outcrops between the Río Grijalva and Río de la Venta, north of Ocozocoautla de Espinosa, Chiapas, at 800 to 1,200 m elevation. Mr. Larry Bussle, a Tampa based horticulturist, claims to have seen *Anthurium clarinervium* along the Interamerican highway in Guatemala, near the Mexican border, but no collections were made to substantiate this report.

The species is a member of section *Cardiolonchium* and is recognized by its broadly ovate, velvety leaf blades with all principal veins much paler than the surface and with a very narrow or closed sinus. The blades have basal veins usually free to the base or coalesced into a short posterior rib that is never marginal.

The species has been confused with *A. leuconeurum,* which also purportedly originates from southern Mexico but whose exact origin is unknown. The latter species is distinguished by having a generally larger, more narrowly ovate blade with an obovate or hippocrepiform sinus and a conspicuously well developed, naked, posterior rib (i.e., it is marginal to the sinus).

Anthurium clarinervium often occurs in mixed stands with *A. pedatoradiatum,* a species that flourishes in the same limestone outcrop habitats in southern Mexico. The two species readily hybridize to form a somewhat intermediate plant, having the velvety texture of *A. clarinervium* but displaying a somewhat shallowly lobed margin representative of *A. pedatoradiatum* (see *Croat 40647*).

In Chiapas the species is known as "Hoja de corazon." It is now widespread in cultivation, at least in the United States.

MEXICO. CHIAPAS: N of Berriozábal, *Breedlove 20274, 24822* (DS); *Breedlove & Dressler 29713* (CAS, DS);

vicinity Ocozocoautla de Espinosa, *Breedlove 9990* (DS, MEXU); *Breedlove 10365* (DS); *Breedlove & Raven 13582* (CAS, DS); *Breedlove 38172* (CAS, DS); *Croat 40646* (MO); *Matuda 25894* (MEXU).

Anthurium clavatum Croat & Baker, Brenesia 16 (Supl. 1): 39. 1979. TYPE: Costa Rica. Cartago: Tapantí Hydroelectric Reserve along Río Grande Orosi, 4.5 km beyond small bridge which crosses the river inside the preserve, along road to diversion dam, elev. 1,500–1,700 m, *Croat 36079* (MO-2381175, holotype; CR, F, NY, US, isotypes; Live at MO).

Epiphytic or terrestrial; stems to 1 m long, 2–3 cm diam.; internodes 1.5–2.5 cm long; roots 1 or 2 per node, ca. 5 mm thick, woolly-pubescent on drying; cataphylls moderately thick, 13–28 cm long, narrowly rounded at apex with a subapical apiculum, drying reddish-brown (B & K Yellow-red 4/10), subpersistent. LEAVES erect-spreading; petioles 90–140 cm long, 1–1.5 cm diam., subterete, narrowly and obtusely sulcate; geniculum 3–3.5 cm long; blades ovate, moderately thick, short-acuminate at apex (the acumen minutely apiculate), deeply lobed at base, 35–70 cm long, 26–50 cm wide, broadest near point of petiole attachment; anterior lobe 25–48 cm long, the margins broadly convex; posterior lobes 12–22 cm long, directed downward; the sinus hippocrepiform, rounded to obtuse at apex; both surfaces semiglossy; midrib convexly raised above, diminished and sunken toward apex, acutely raised below; basal veins 5–7 pairs, up to 5 of them coalesced 2.5–6 cm, raised above and below, the posterior rib broadly curved, naked; primary lateral veins 4–7 per side, departing midrib at ca. 55° angle, then spreading at 35°–45° angle, loop-connected, sunken above, raised below; lesser veins less conspicuous; collective vein arising from uppermost basal vein, 5–15 mm from the margin. INFLORESCENCE usually slightly shorter than or about as long as the leaves; peduncle 43–110 cm long, to ca. 8 mm diam. midway, half as long as or equalling the petioles; spathe moderately coriaceous, pale green (B & K Yellow-green 8/7.5), ovate-elliptic, 7–12 cm long, 3.5–5 cm wide, broadest 1–2 cm above point of attachment, cuspidate-acuminate at apex (the acumen inrolled, 6–10 mm long), acute to obtuse at base, inserted on peduncle at ca. 80° angle; stipe 1–6 cm long in front, 2–8 mm long in back, ca. 6 mm diam.; spadix clavate, green (B & K Yellow-green 8/10) to orange-tan, 4.5–7.5 cm long, 1.2–1.5 cm diam. at base, 1.5–2.2 cm diam. at apex; flowers 4-lobed, (1.4)2.3–2.7 mm (dry) in both directions, the sides sigmoid; 20 or more flowers visible in the principal spiral, 13–16 flowers visible in the alternate spiral; tepals semiglossy, the lateral tepals 1.2–1.3 mm wide (dry), the inner margin broadly rounded; pistil emergent but not raised, green; stigma oblong-elliptic, slitlike, ca. 0.5 mm long; stamens emerging, scattered, beginning near the middle, the lateral stamens exserted throughout the spadix before the alternates emerge; anthers white, held in a moderately close circle, contiguous or nearly so at upper edge of tepals, ca. 0.4 mm long and 0.5 mm wide; thecae ovate, moderately divaricate; pollen white. Immature INFRUCTESCENCE to 10 cm long and 3.3 cm wide; berries not seen. Figs. 47 and 48.

The species is known only from central Costa Rica on the Atlantic slope of the Cordillera de Talamanca in the region of the type locality. It inhabits lower montane rain forest from 1,300 to 1,800 m elevation.

Anthurium clavatum belongs in section *Calomystrium* and is perhaps most closely related to *A. fraternum* Schott, *A. hoffmanii,* and *A. nymphiifolium* C. Koch & Bouché, which all share thick, persistent cataphylls. *Anthurium clavatum* differs from all of these by its clavate spadix. Another distinguishing feature is the broad spathe with a long cusp.

COSTA RICA. CARTAGO: no other location, *Utley & Utley 1624* (F); above the Río Grande de Orosi, S of Tapantí, *Cochrane et al. 6334* (F); *Lent 940* (CR, F); *998* (F); SE of Orosi, above Finca La Concordia, *Lellinger & White 1508* (CR, F, US); road from Tapantí to Taus-Tausito, beyond bridge over Río Grande de Orosi at Tapantí, *Utley & Utley 5616* (DUKE); Tapantí Hydroelectric Reserve, *Croat 36079* (CR, F, MO, NY, US), *47050* (MO); road between Trinidad and Hacienda El Volcan Turrialba, *Luteyn 3259* (DUKE).

Anthurium clavigerum Poepp. in Poepp. & Endl., Nov. Gen. & Sp. 3: 84. 1845. TYPE: Peru. Pampayacu, *Poeppig 1423* (W, not seen; F, photo).

Anthurium panduratum Mart. ex Schott, Oesterr. Bot. Wochenbl. 5: 273. 1855. TYPE: Brazil. Rio Negro. *Martius 3115* (M, not seen; US, photo).

Anthurium holtonianum Schott, Oesterr. Bot. Wochenbl. 7: 317. 1857. TYPE: Colombia. La Paila. *Holton s.n.* (K, not seen; SEL, photo).

Anthurium repandum Schott, Oesterr. Bot. Wochenbl. 7: 317. 1857. TYPE: Colombia. Santa Marta. *Purdie s.n.* (K, not seen; SEL, photo).

Anthurium wendlandii Schott, Oesterr. Bot. Z. 8: 182. 1858. TYPE: Costa Rica. San Miguel, *Wendland 957* (GOET).

Anthurium kalbreyeri N. E. Brown, Gard. Chron. pt. 2: 117. 1881. TYPE: Colombia. Antioquia, *Kalbreyer s.n.* (K, not seen).

Anthurium burchellianum (Engl.) Macbr., Field Mus. Nat. Hist., Bot. Ser. 11: 7. 1931.

Anthurium panduratum var. *burchellianum* Engl., Pflanzenr. IV 23 B: 279. 1905. TYPE: Brazil. Pará, *Burchell 9632* (K, not seen).

Anthurium obovatum Gleason, Bull. Torrey Bot. Club 56: 9. 1929. TYPE: Br. Guiana. Kopinang River, Anandabaru, *Alston 475* (K, not seen; F, photo).

Anthurium monsteroides Steyerm., Fieldiana, Bot. 28: 93. 1951. TYPE: Venezuela. Mérida: Río Onia near Bolero, N. of Mesa Bolívar, *Steyermark 56727* (F).

Epiphyte; scandent; stems 2 m long, 3–4 cm diam.; roots dense, 3–10 mm diam., brownish-green; cataphylls coriaceous, to 12 cm long, weathering to medium brown fibers, ultimately deciduous. LEAVES erect-spreading; petiole 65–150 cm long, terete or weakly sulcate; geniculum 1.5–2 cm long; blades digitately discoid to reniform in outline, to 2 m wide, the leaflets 25–100 cm or more long, 4–12 cm wide, sinuate or lobate, acuminate at apex, acute at base, the upper surface matte, the lower surface semiglossy; the midrib of the leaflets convexly raised above and below, diminished and sunken at apex above; the primary lateral veins 3–4 per side, raised in valleys above, raised below, departing midrib at 45° angle, arcuate-ascending to form collective vein in apical portion of leaflet. INFLORESCENCE arching-pendent; peduncle to 90 cm long, terete, shorter than petioles; spathe coriaceous, violet-purple, lanceolate, 30–65 cm long, 3–11 cm wide; spadix lavender-purple (B & K Purple 6/2.5), 20–75 cm long, to 2 cm diam. at base, to 9 mm diam. at apex; flowers rhombic, ca. 3 mm in both directions, the sides straight to slightly sigmoid; ca. 14 flowers visible in the principal spiral, ca. 8 flowers visible in the alternate spiral; tepals matte; pistil emergent but not raised, lavender; stigma linear, darker purple than pistil; stamens emerging from base, covering pistil; anthers purplish-brown; thecae irregular, not divaricate; pollen white to pinkish. INFRUCTESCENCE pendent; berries obovate, purple, developing in basal portion only, seeds 1–2, white, oblong. Figs. 49 and 50.

Anthurium clavigerum is found from Nicaragua to the Guianas, Brazil, and Bolivia. In Costa Rica it occurs in premontane wet forest and tropical wet forest life zones at sea level to 700 m. In Panama, the species also occurs in premontane moist forest and tropical moist forest. It has also been collected at a reportedly 1,000 m elevation in what is apparently lower montane wet forest or lower montane rain forest.

This species is not confused with any other in Central America and can be recognized by its pedatisect leaves with sinuate to lobed margins and by its huge pendent inflorescence. The species may have leaf blades to about 2 m broad making it the largest species of *Anthurium* in Central America. It is a member of section *Dactylophyllium* and is most closely related to *A. sinuatum* Benth. ex Schott of South America.

COSTA RICA. ALAJUELA: vicinity Artezalea, NE of Villa Quesada, *Molino et al. 17843* (F, NY); between Cañas and Upala, NNE of Bijagua, *Croat 36291* (MO); S of Canalete near Río Zapote, *Burger & Baker 9963* (F, MO); vicinity Colonia Blanca, *Almeda & Nakai 4002* (MO); vicinity Volcán Arenal, *Lent 2672* (F, MO). LIMÓN: NE of Bribrí, *Croat 43244* (MO); Hacienda Tapezco & Hacienda La Suerte, W of Tortuguero, *Davidson et al. 7135* (LAM); *Donahue 8500* (MO); between Limón and Puerto Viejo, *Baker & Burger 176* (DUKE, F, MO, NY). PUNTARENAS: above Golfito, *Burger & Matta 4770* (F, NY); Playa Blanca Road near Rincón de Osa, *Liesner 2153* (MO); SW of Rincón de Osa, *Raven 20864* (CAS, NY).

NICARAGUA. RÍO SAN JUAN: near Caño Chontaleño, NE of El Castillo, *Neill 3378* (MO). ZELAYA: along Río Escondido, N of Bluefields, *Harmon & Fuentes 5083* (MO); vicinity Siuna, at Caño Majagua, *Neill 1818* (MO); *Stevens 6882* (MO); trail from Cerro Saslaya to San José del Hormiguero, *Stevens 7067* (MO); S of bridge at Colonia Agrícola Yolaina on road to Colonia Manantiales, *Stevens 4856* (MO); road to Colonia Agrícola Yolaina & Colonia La Esperanza, *Stevens 6363* (MO); along Río Sucio, *Stevens 8028* (MO); SW of Río Wawa ferry on road from Puerto Cabezas to Rosita, *Stevens 7904* (MO); near Río Okanwás, E of Rosita, *Neill 4433* (MO); between Rosita and Puerto Cabezas, *Stevens 8501* (MO); NE of Siuna, along Caño-Madriguera, *Neill 3727* (MO).

Anthurium clidemioides Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 3. 1940. TYPE: Costa Rica. Alajuela: Villa Quesada, San Carlos, altitude 800 m, *Valerio 1726* (F-933729, holotype).

Epiphyte; stem scandent; internodes elongate, 2–15 cm long, 2–3 mm thick, covered with corky, lenticel-like tubercles; cataphylls absent. LEAVES spreading; petioles 2–5.5 cm long, sheathed half their length or less, the base encircling the stem, narrowly flattened with a medial ridge adaxially, faintly multi-ridged abaxially; geniculum less than

FIGURES 50–53. 50. *Anthurium clavigerum* Poepp., *Croat 4654.*—51. *Anthurium clidemioides* Standl. *Daniels s.n.*—52. *Anthurium concinnatum* Schott, *Croat 26493.*—53. *Anthurium cordatotriangulum* Matuda. *Matuda 38276* (Type).

5 mm long, weakly tuberculate; blades ovate-cordate, bullate, chartaceous, acuminate at apex, lobed at base, 7–14 cm long, 4–9.5 cm wide, broadest 1–2 cm above point of petiole attachment; the anterior lobe 6–11 cm long; the posterior lobes rounded, 1–2 cm long; the upper surface matte; basal veins 4–5 pairs, sunken above; the lower surface paler; collective vein arising from the first basal vein. INFLORESCENCE spreading; peduncle obscured by base of spathe or rarely to 5 cm long; spathe green, lanceolate, ca. 5 cm long, ca. 1 cm wide; spadix purplish, 4.2–6 cm long, 5–7 mm diam. at base, 3–4 mm diam. at apex: the flowers rhombic to 4-lobed, 5.3 mm long, 3.5 mm wide; 3–5 flowers visible in the principal spiral, 4–5 flowers visible in the alternate spiral; tepals semiglossy; pistil weakly raised; stigma punctiform, ca. 0.6 mm diam. INFRUCTESCENCE spreading-pendent; berries orange, obovoid-oblong-ellipsoid, (5)8–9 mm long, 4–6 mm wide, drying dark maroon; seeds (1)2–6, obovate-elliptic, flattened, brown or black, 7 mm long, 3.5 mm wide. Fig. 51.

This species is known from the Atlantic and Pacific lowlands of Costa Rica in tropical wet forest from sea level to 800 m elevation.

Anthurium clidemioides is placed in section *Polyphyllium* (Croat & Baker, 1978) and is easily one of the most distinctive species of *Anthurium* due to its bullate leaves and near absence of a peduncle. In its sterile state, it could be mistaken for species of *Piper, Dioscorea, Pilea,* or even some Melastomataceae.

COSTA RICA. ALAJUELA: San Carlos, Villa Quesada, *Valerio 1726* (F). HEREDIA: Finca La Selva, Puerto Viejo, *Hartshorn 939* (MO); *Moore 9998* (BH); *Opler 2091* (F). LIMÓN: Hacienda Tapezco and Hacienda La Suerte, W of Tortuguero, *Davidson & Donahue 8735, 8824* (MO). PUNTARENAS: Corcovado National Park, *Liesner 2922* (MO).

Anthurium concinnatum Schott, Prod. Aroid. 522. 1860. *Anthurium bogotense* Schott var. *concinnatum* (Schott) Engl., Monogr. Phan. 2: 184. 1879. TYPE: Costa Rica. Cartago: Turrialba, *Oersted s.n.* (Photo of Schott Aroid Drawing #709; NYBG Neg. #N.S. 3905).

Usually epiphytic or sometimes terrestrial; stems to 1 m or more long, 2.5–4 cm diam.; internodes obscured by weathering cataphylls; cataphylls coriaceous, 7–15 cm long, drying brown, splitting at base, remaining intact at apex. LEAVES erect to spreading; petioles subterete, weakly and bluntly sulcate, 35–75 cm long, 0.6–1.2 cm diam.; geniculum 1.5–3 cm long; blades subcoriaceous, narrowly ovate, 37–58 cm long, 21–34 cm wide, abruptly acuminate at apex, deeply lobed at base; the sinus spathulate, the lobes often overlapping; both surfaces glossy; the midrib and primary lateral veins raised above and below, lesser veins prominulous; basal veins to 7 pairs, all basal veins coalesced to 1.5 cm; the collective vein arising from the first basal vein, loop-connecting the primary lateral veins and running to apex. INFLORESCENCE spreading-pendent; peduncle 35–65 cm long, shorter than petioles; spathe oblong-lanceolate, pale green turning purplish, 8.5–27 cm long, 1.5–5 cm wide, abruptly cuspidate at apex; stipe to 2.5 cm long, sometimes arching; spadix green turning purplish, 5–26 cm long, sometimes arched at base, 8–16 mm diam. at base, 3–8 mm diam. at apex; flowers rhombic; 8–9 flowers visible in the principal spiral, 12 or more flowers visible in the alternate spiral; pistils raised; stamens well exserted, held at the edge of tepals and ± above pistil; anthers white; thecae brown, persistent, giving spadix spiny appearance. INFRUCTESCENCE pendent; spadix to 30 cm long; berries orange; mesocarp pulpy, orange with numerous, linear raphide cells; seeds 1–2 obovoid, 4.3 mm long, 3.5 mm wide, pale yellow, indented at base, darker area at apex. Figs. 52 and 54.

The species is found in Costa Rica and possibly also in Colombia and Ecuador at elevations of 2,000 to 3,000 m in lower montane rain forest. The species grows at higher elevations than any other *Anthurium* in Costa Rica or Panama.

Anthurium concinnatum is a member of section *Belolonchium* and is recognized by its large, subcoriaceous, cordate blade and its curved stipe, its persistent, exserted stamens and high altitudinal range. The species usually has long stems that, although sometimes rooted in the soil, are usually leaning on trees for support.

COSTA RICA. ALAJUELA: Volcán Poás, *Lems s.n.* (NY). CARTAGO: Cerro Carpintera, *Standley 34416* (US); Cerro de La Muerte, *Croat 35378, 35407* (MO); near El Cañón, S of Cartago, *Williams et al. 28244* (NY, US); vicinity El Empalme, *Almeda & Nakai 3807* (MO); *Almeda 3823* (CAS); *Wilbur et al. 16151, 16175* (Duke); *Lems s.n.* (NY, US); NE of El Retiro, *Almeda & Nakai 3788* (MO); La Estrella, *Standley 39515* (US); Irazú National Park, *Davidson 8231* (MO); *Pittier 4401* (BR);

FIGURES 54–57. 54. *Anthurium concinnatum* Schott, *Croat 26326*. — 55–56. *Anthurium consobrinum* Schott, *Baker 151*. — 57. *Anthurium cotobrusii* Croat & Baker, *Croat 48850*.

vicinity Poás, *Tonduz 10681* (BR). CARTAGO & SAN JOSÉ BORDER: along Interam Highway, *Burger & Liesner 6479* (F, MO); *7018* (F, NY); *Burger & Baker 9537* (F, DUKE); *Luteyn 2975* (DUKE); *Raven 20945* (MO); Tablazo, *Brade 2537* (BR). HEREDIA: Cerro Caricias, N of San Isidro, *Standley & Valerio 52301* (US); between Cerro Chompipe & SE slope of Volcán Barba, *Baker et al. 238* (F, MO); Volcán Barba, *Pittier & Durand 1345* (BR); *Utley 4571, 4572, 4573* (DUKE). PUNTARENAS: vicinity Boruca, *Pittier 10483* (BR). SAN JOSÉ: no other location, *Jiménez 937* (US); vicinity Aserri, *Almeda 3672* (CAS); western ascent to Cerro de la Muerte, *Croat 32854, 32892* (MO); near Finca La Cima, N of Copey, *Standley 42059, 42636* (US); La Lagunilla, *Pittier 10447* (BR, US); NE of Santa María de Dota, *Standley 42241* (US); near Vaca & Chino, *Dodge & Thomas 5422* (MO).

Anthurium consobrinum Schott, Oesterr. Bot. Wochenbl. 5: 66. 1855. TYPE: Nicaragua, Dept. of Río San Juan, Río San Juan, *Friedrichsthal s.n.* (Photo of Schott Aroid Drawing #353; NYBG Neg. #N.S. 3874).

Rosulate epiphyte; stems short, 1.5–2 cm diam.; roots very dense, short, ascending, narrowly tapered, white to greenish white; cataphylls subcoriaceous, 5.5–15 cm long, caudate-acuminate at apex, drying rusty brown (B & K Yellow 6/2.5), persisting intact, ultimately deciduous. LEAVES erect; petioles broadly sulcate, rounded abaxially, 2.5–9 cm long, 0.6–1 cm diam.; geniculum 0.5–2 cm long; blades oblanceolate, subcoriaceous, 19–64 cm long, 3.5–20 cm wide, abruptly acuminate at apex, acute to narrowly rounded at base; both surfaces matte to semiglossy; the midrib flat at base above, acutely raised toward apex, convexly raised below; primary lateral veins 12–18 per side, raised above and below, departing midrib at 40° – 60° angle, straight to near margin then arching and joining margin; collective vein lacking or arising from one of the primary lateral veins near middle of blade, 5–12 mm from margin. INFLORESCENCE erect to arching, shorter than leaves; the peduncle 20–43 cm long, 5–6 mm diam., several times longer than petioles, terete; spathe linear-lanceolate, subcoriaceous, green, 4.5–7.5 cm long, 0.8–2.5 cm wide, abruptly acuminate at apex, round to truncate at base; spadix greenish-white, turning pinkish-tan, strongly curved, 6–9 cm long, 1–1.5 cm diam.; the flowers 4-lobed, 2.7–3.4 mm in both directions, the sides weakly to jaggedly sigmoid; 11–15 flowers visible in the principal spiral, 15–16 flowers visible in the alternate spiral; tepals matte; the pistil pyramidal and exserted to 2.2 mm; the stigma ellipsoid, 0.5–0.7 mm long, becoming brushlike; stamens emerging slowly from base of spadix, exserted on fleshy, colorless filaments ca. 1 mm long, then retracting to surface of tepals; anthers ovate-triangular, white, 0.8–1 mm long, 0.8–1 mm wide; thecae narrowly ovate; pollen white. INFRUCTESCENCE pendent; spadix to 13 cm long; berries translucent, greenish-white with apex reddish to purplish, narrowly acute to prominently beaked, ca. 1 cm long, 5 mm wide; mesocarp juicy; seeds 2, greenish-white, oblong-elliptic, 3–3.4 mm long, ca. 2 mm wide, 1.5 mm thick, enveloped in a gelatinous, transparent envelope that extends ca. 1 mm beyond seed on both ends, broader at apex. Figs. 55 and 56.

The species ranges from Nicaragua to Costa Rica from sea level to 700 m elevation. It is a common species from tropical wet forest and premontane wet basal belt transition life zones on the Caribbean slope. It is to be expected in Panama in Bocas del Toro Province.

The species is distinguished by its rosulate habit, oblanceolate blades, short sulcate petioles, massive whitish root system, spreading inflorescence with upturned, nontapered spadix, markedly protrudant styles, and berries that are greenish-white at the base and reddish at the apex.

Anthurium consobrinum is probably most closely related to *A. fatoense* of Costa Rica and Panama and differs from that species by its abaxially rounded petioles, by its nearly oblong spadix, and by berry coloration. *Anthurium fatoense* has a quadrangular petiole, a cylindroid-tapered spadix, and pale yellow or orange berries. *Anthurium consobrinum* was placed in section *Episeiostenium* by Schott but is probably a member of section *Pachyneurium*.

COSTA RICA. no other location, *Proctor 32168* (LL); *Taylor 11593* (NY). ALAJUELA: vicinity of Bijagua, *Almeda & Nakai 4043* (MO); *Burger & Baker 9857* (DUKE, F, MO, NY); *Croat 36264, 36423* (MO); *Utley & Utley 3907* (DUKE, MO); road between Cañas & Upala near Río Zapote, *Croat 36383* (MO); NE of Interamerican Highway toward Upala, *Wilbur 20094* (DUKE); west of La Marina, *Molina et al. 17329* (NY, US); between Naranjo & Aguas Zarcas, NE of Quesada, *Croat 46949* (MO); Santa María National Park, *Liesner 5072* (MO); Zapote, *Taylor 18163* (NY); Finca Los Ensayos, NW of Zarcero, *Croat 43615* (MO). HEREDIA: near Puerto Viejo, *Croat 35671, 35695* (MO); *Taylor 4571* (NY); *Burger & Stolze 5934* (PMA); near Tirimbina, E of Río Sarapiquí, *Burger & Burger 8090* (F, MO). LIMÓN: road between Cahuita & Limón, *Baker & Burger 151* (F, MO); Finca Castilla, *Dodge & Goerger s.n.* (MO); Hacienda Tapezco & Hacienda La Suerte,

W of Tortuguero, *Davidson & Donahue 6723, 6768, 8413, 8461, 8733* (MO).

NICARAGUA. RÍO SAN JUAN: near Caño Chontaleño, NE of El Castillo, *Neill 3332, 3376, 3420, 3421* (MO); *Neill & Vincelli 3622* (MO). ZELAYA: Bluefields, N of Base Camp, *Proctor et al. 26913, 27010* (LL, MICH, NY, US); Caño Costa Riquita, SW of Colonia Naciones Unida, *Stevens 4966, 5058, 6411, 6412* (MO); Caño Zamora on Río Rama, *Stevens 8861* (MO); S of bridge at Colonia Agrícola Yolaina, *Stevens 4819, 4826, 6308* (MO); road to Colonia Agrícola Yolaina & Colonia La Esperanza, *Vincelli 166, 168* (MO); Salto La Oropéndola, *Stevens 8954* (MO).

Anthurium cordatotriangulum Matuda, Anales Inst. Biol. Univ. Nac. México 36: 109. 1966. TYPE: Mexico. Chiapas: Motozintla; Sierra Madre de Chiapas, El Rosario (ca. 8 mi S of Motozintla), 1,800 m elev., *MacDougall 393* (MEXU, holotype).

Stems short; cataphylls broadly triangular, 5–7 cm long, drying and weathering into persistent fibers. LEAVES with petiole 50–55 cm long, 5–8 mm diam., broadly sulcate, stiff; geniculum 2–3 cm long; blades broadly ovate-triangular, subcoriaceous, gradually acuminate at apex, broadly lobed at base, 37–64 cm long, 26–46 cm diam., broadest at point of petiole attachment or just below; the anterior lobe 30–44 cm long; the posterior lobes 11–23 cm long, directed outward at ca. 45° angle from petiole; the sinus parabolic to hippocrepiform, round at apex; the midrib raised above and below; basal veins 5 or 6 pairs, the third to sixth coalesced 3–6 cm, raised above and below; primary lateral veins 5 or 6 per side, departing midrib at 60° angle, ± straight, usually prominently loop-connected into collective vein in apical half of blade; the collective vein arising from the first basal vein or sometimes from one of the lower primary lateral veins. INFLORESCENCE usually longer than leaves; peduncle subterete, to 57 cm long, ca. 5 mm diam.; spathe moderately thick, green, lanceolate, 14–18 cm long, 2.5–4.5 cm wide, long-acuminate at apex, rounded and ± clasping at base; stipe to 15 mm long in front, 6 mm long in back; spadix purplish (dried), 10–13 cm long, 8–10 mm diam. at base, 4–5 mm diam. at apex; the flowers rhombic, 2.7–3.1 mm long, 1.5–2.2 mm wide; 7–9 flowers visible in the principal spiral; tepals weakly punctate; pistils not emergent; stigma 3–3.5 mm long, broadly elliptic; stamens emerging from base and held just above tepals in a tight cluster; thecae oblong-elliptic, scarcely divaricate. INFRUCTESCENCE not seen. Figs. 53 and 58.

Anthurium cordatotriangulum is known for certain only from the southeastern corner of Chiapas near the Guatemalan border in Motozintla and Unión Juárez in the Sierra Madre de Chiapas at 1,800 to 1,900 m in oak-pine forest. Two other closely related species, *A. montanum* and *A. chamulense,* have been collected at the type locality of *A. cordatotriangulum.* A collection from San Carlos Yautepec in the Sierra de Lacheguia in South Central Oaxaca matches the type of *A. cordatotriangulum* very well but it is difficult to explain the otherwise apparent endemism of this species. (This specimen bears the unpublished herbarium name of *A. oaxacarupicolum* Matuda but since the collection differs in no appreciable way from *A. cordatotriangulum* it will not be recognized here.) The region around San Carlos Yautepec is very arid and nearly devoid of habits for *Anthurium.* I suspect that the label data referring to San Carlos Yautepec was intended to refer to the municipio of the same name which is very large and no doubt includes good *Anthurium* habitats in the southern part.

The species is placed in section *Belolonchium* and is distinguished by its almost deltoid blades, its coarsely elevated basal and primary lateral veins (on drying), broad ovate-lanceolate spathe, and long-tapered, violet-purple spadix. Although Matuda compared the species with *A. macdougalii* (*A. andicola*), it is perhaps most easily confused with *A. montanum,* which occurs in the same area in southeastern Chiapas, but that species differs in having narrowly ovate blades, scarcely raised veins (on drying), a generally much smaller spathe, and a spadix that is less conspicuously long-tapered.

MEXICO. CHIAPAS: El Rosario, *MacDougall 393* (MEXU); *Matuda 38628* (MEXU); Volcán Tacaná, *Matuda 38626* (MEXU). OAXACA: San Carlos Yautepec, *Matuda 38276* (MEXU).

Anthurium cotobrusii Croat & Baker, Brenesia 16 (Supl. 1): 43. 1979. TYPE: Panama. Chiriquí: above San Felix, along mining road, 18–27 miles off Pan-American Highway (above Chamé on turnoff to Escopeta), elev. 1,200–1,500 m, *Croat 33058* (MO-2381190–91, holotype; CR, F, NY, US, isotypes; Live at MO).

Terrestrial or sometimes epipetric or epiphytic; stem 1–3 cm diam. usually less than 15 cm long; roots greenish or grayish-brown, thick and

FIGURES 58–61. 58. *Anthurium cordatotriangulum* Matuda, *MacDougall 393* (Type).—59–60. *Anthurium cotobrusi* Croat & Baker, *Croat 33058* (Type).—61. *Anthurium cubense* Engl., *Neill 2730*.

smooth, to ca. 6 mm diam.; cataphylls 9–11 cm long, green, sometimes tinged purplish, turning tan, ultimately weathering to fine persisting fibers. LEAVES erect-spreading; petioles 15–65 cm long, 5–7 mm diam., ± terete, weakly sulcate or flattened; geniculum 1–3 cm long; blades narrowly ovate to triangular, subcoriaceous, narrowly long-acuminate at apex, the acumen often turned down sharply, shallowly and broadly lobed at base, 16–56 cm long, 9.5–25 cm wide, widest at the base; the anterior lobe (13)18–30(37) cm long, the margin ± straight to convex; the posterior lobes (5)8–11(15) cm long, turning up; the sinus much broader than deep when flattened, obtuse to acute at apex; both surfaces semiglossy; midrib obtusely raised on both surfaces at base, more sharply raised toward apex on upper surface, finally diminishing at apex; primary lateral veins 5–8 per side, weakly to sharply raised (especially toward base) above, weakly raised below, arcuate-ascending; basal veins 3–5 pairs, 3 or 4 of them coalesced 4–6 cm; posterior rib naked throughout its length, gradually curved to almost straight, turning under; lesser veins less conspicuous; the collective vein arising from the lowermost primary lateral vein, from a primary lateral vein above the middle or from the first basal vein. INFLORESCENCE erect-spreading, shorter to longer than the leaves; peduncles terete, (4.5)20–46 cm long; spathe green, pale green, or green with purplish veins or heavily suffused with purple on inner surface, sometimes tinged purple only at base medially, ovate to narrowly ovate, (2.5)5–9.5(12) cm long, (1.7)2.7–4.5 cm wide, weakly boat-shaped to flat, acuminate at apex, acute to rounded or shallowly cordate at the base, inserted at 60°–70° angle on peduncle; stipe green or green tinged with purple, 10–20 mm long in front, 2–6 mm long in back; spadix green to dark purple-violet at anthesis, (2.5)5–25 cm long, 7–15 mm diam. at base, 3–7 mm diam. at apex, with a pungent, sweet scent when droplets are fresh; flowers sub-4-lobed, 3.5–5 mm long, 3.5–4 mm wide, sometimes ca. 3.5 mm in both directions; 3–6 flowers visible in the principal spiral, 7–10 flowers visible in the alternate spiral; tepals dark violet-purple or yellow-green with purple margins, sparsely punctate, more densely so near margins, semiglossy to matte, the inner margins broadly convex; pistil green; stigma linear, purple-violet or green, ca. 0.6 mm long, forming conspicuous droplets for 1–3 weeks before emergence of stamens, droplets persisting when the first and second stamens are opening; stigma drying and covered by thecae when third and fourth stamens are emerged; stamens weakly exserted in a close circular cluster; anthers orange to yellowish, held just above the tepals, 0.6–0.9 mm long, 1 mm wide; filament short, retracting; pollen pale orange, fading white. INFRUCTESCENCE erect-spreading; berries pale orange (B & K Yellow-red 8/7.5), obovoid, 12–15 mm long, 8–11 mm diam., rounded at apex, the apex darker, depressed with 4 short, slightly elevated ridges; mesocarp juicy, orange; seeds usually 2, oblong-elliptic, 6.5–7.5 mm long, 2.5–4 mm wide, encased in a flattened, translucent envelope that projects up to 3 mm beyond the apex of the seed and up to 1 mm beyond the lateral margins. Figs. 57, 59, and 60.

Anthurium cotobrusii is found in Costa Rica and Panama in premontane wet forest at elevations of 1,000 to 1,500 m.

This species is most easily distinguished by its subcoriaceous leaves which have more or less obscure reticulate veins when fresh but have conspicuous reticulate veins when dry, and by its prominently tapered, violet-purple spadix with a tight cluster of stamens. In a dried state the flowers have their tepals turned somewhat upwards, which, in conjunction with the clustered stamens, gives the spadix a rough appearance. Other diagnostic features are the primary lateral veins often free to the margin in the basal half of the blade, the thick, grayish roots that are densely long-pubescent on drying and the early emergent berries that are quadrangular with prominent ridges radiating from the center to the corners.

The species is now placed in section *Belolonchium*. It was erroneously placed previously in the section *Cardiolonchium* by Croat and Baker, 1980. It is most easily confused with *A. ranchoanum*, which has similar leaves, but the latter has a short cylindroid, scarcely tapered spadix that is usually nodding and hooded by the spadix when in flower (the spathe remaining erect in fruit). In contrast, *A. cotobrusii* has an erect, prominently tapered spadix and a prominently reflexed spathe. In addition, the berries of *A. ranchoanum* are smoothly rounded at apex.

COSTA RICA. PUNTARENAS: above coffee fincas along Río Coto Brus, near Cotán, N of La Unión (on Panama border), *Croat 26674* (MO).

Anthurium cubense Engl., Bot. Jahrb. Syst. 25: 364. 1898. TYPE: Cuba. Ad Monte Toro, alt.

300 m, *Eggers 5402* (K, holotype; B, isotype).

Epiphytic or terrestrial; to 40 cm tall; stem short, to 3 cm diam.; roots green, pubescent at base, to 8 mm diam., ascending at upper nodes; cataphylls subcoriaceous, to 6 cm long, drying brown, remaining ± intact and persisting between leaves. LEAVES rosulate, erect; petioles 5–10 cm long, 5–11 mm diam., subterete or obscurely quadrangular, broadly sulcate; geniculum 0.5–1 cm long, sometimes tinged purplish; blades oblanceolate-elliptic, subcoriaceous, gradually acuminate at apex, obtuse to narrowly rounded at base, 26–83 cm long, 9–25 cm wide; the upper surface semiglossy; the midrib bluntly raised above and below; primary lateral veins 6–7 per side, raised above and below; lesser veins less conspicuous. INFLORESCENCE erect; peduncle 8–16 cm long, 5–6 mm diam., terete, green suffused with violet; spathe subcoriaceous, subovate, olive green, tinged with violet-purple at margins, 2.5–16 cm long, 0.6–5 cm wide; spadix weakly ellipsoidal, 5.5–10 cm long, 0.8–1 cm diam. midway, white or lavender (B & K Purple 6/7.5); flowers rhombic or weakly 4-lobed, 2.1–2.5 mm long, 2.4–2.6 mm wide, the sides weakly sigmoid; 9–12 flowers visible in the principal spiral, 14–16 flowers visible in the alternate spiral; tepals matte, lateral tepals 1.2–1.4 mm wide; pistil weakly raised, greenish; stigma linear to 0.4 mm long; stamens emerging in scattered pattern throughout, the lateral stamens emerging almost to the apex before third or alternates emerge, held just above tepals against pistil, obscuring pistil when all stamens develop; anthers white tinged red-violet; thecae oblong; pollen white. INFRUCTESCENCE spreading; berries red, oblong-elliptic, 9–12 mm long, 4.5–6 mm wide; seeds 1 or 2, 5–5.5 mm long, 3 mm wide. Figs. 61 and 62.

Anthurium cubense is found in Cuba, Yucatan, and drier parts of eastern Guatemala on the Atlantic slope; also Nicaragua to Panama along the Pacific slope. The species is also known from northern Colombia and Venezuela. It is known from tropical dry forest and drier parts of tropical moist forest at low elevations. The species is apparently rare except in Nicaragua where it is locally common.

Anthurium cubense is placed in section *Pachyneurium* and is recognized by its short petioles, short inflorescences (much shorter than the leaves; the peduncle as short as or only slightly longer than the spadix), its cylindroid, pale violet-purple spadix usually weakly tapered toward both ends, and its bright red berries.

Engler (1905) also recognized material of this species under the name *A. recussatum* Schott from Cuba. That name, however, has been misapplied and actually refers to *A. hookeri* Kunth from the Lesser Antilles and northeastern South America. *Anthurium hookeri* is not related to *A. cubense*, although it has a similar rosulate habit. It differs chiefly in having punctate leaves with unusual scaliform secondary veins and by having supervolute vernation.

COSTA RICA. GUANACASTE: S of Peñas Blancas, *Liesner 4652* (MO). PUNTARENAS: vicinity of Cabo Blanco Nature Reserve, *Burger & Liesner 6627* (F, MO).

GUATEMALA. ALTA VERAPAZ: Cubilhuitz, *Tuerckheim 8606* (US).

NICARAGUA. CHONTALES: S of Acoyapa, *Nichols 1725* (MO); N of Cuapa, *Stevens 3662, 6107* (MO); *Vincelli 86, 87* (MO). GRANADA: NE side of Volcán Mombacho, *Atwood & Neill AN82* (MO); *Neill 2730* (MO). MANAGUA: vicinity of Managua, *Maxon et al. 7538* (US). MASAYA: Volcán Masaya National Park, *Stevens 4444* (MO). RIVAS: Isla de Ometepe on Volcán Masearas near Santa Cruz, *Stevens 6626* (MO). ZELAYA: along Caño Majagua, *Stevens 6894* (MO).

Anthurium cuneatissimum (Engl.) Croat, comb. nov. *Anthurium consobrinum* var. *cuneatissimum* Engl., Pflanzenr. IV 23B: 176. 1905. TYPE: Costa Rica. Limón: Llanuras de Santa Clara, 250 m, *Donnell Smith 6811* (B, holotype; US, isotype).

Epiphyte; stems very short; roots dense, descending, fuzzy (dried), ca. 3 mm thick; cataphylls coriaceous, 6–9 cm long, acuminate at apex, drying tan (B & K Red 9/10), weathering into longitudinal fibers. LEAVES erect-spreading; petioles usually quadrangular with sharp edges, sometimes bluntly angular abaxially, often with a sharp medial rib abaxially, 6–32(40) cm long, 5–7 mm wide; geniculum 0.8–2.5 cm long; blades obovate-elliptic, subcoriaceous; (20)25–60 cm long, 8.5–21 cm wide, long-acuminate at apex, acute to cuneate at base; upper surface semiglossy to glossy, lower surface semiglossy; the midrib broad, scarcely raised above, sometimes with a weak medial rib, narrowing and sunken at apex, prominently raised below, sometimes with 1–2 sharp ribs; primary lateral veins (5)10–15 per side, departing midrib at 30°–40° angle, ± straight to collective vein or weakly arcuate-ascending, raised in shallow valleys above, raised

FIGURES 62–65. 62. *Anthurium cubense* Engl., *Neill 2730*. —63. *Anthurium cuneatissimum* (Engl.) Croat, *Croat 36480A*. —64. *Anthurium cuspidatum* Mast., *Croat 27165*. —65. *Anthurium cuspidatum* Mast., *Croat 34145*.

below; lesser veins flat above, flat and conspicuous below; collective vein arising from one of the primary lateral veins, 1–3 mm from the margin. INFLORESCENCE erect-spreading, usually shorter than leaves; peduncle 21–58 cm long, sharply 1-ribbed abaxially, 2–4-ribbed from base to just above middle; spathe ovate, cucullate, dark green, coriaceous, 2.5–6(9) cm long, 2.1–4 cm wide, abruptly to gradually acuminate at apex, rounded to truncate at base, inserted at 50°–70° angle on peduncle; spadix sessile, clavate, pale yellow-green or lemon-yellow, 1.9–5 cm long, ca. 8 mm diam. midway, weakly tapered at base, round at apex; flowers 4-lobed, 1.6–2.2 mm long, 2–2.5 mm wide, the sides jaggedly sigmoid; 16–20 flowers visible in the principal spiral, 13–16 flowers visible in the alternate spiral; tepals matte, conspicuously papillate, lateral tepals 0.6–0.9 mm wide, the inner margin straight to convex and turned up against pistil; the pistil emergent to 0.5 mm, white to pale greenish-white; stigma brushlike, ca. 0.2 mm long, with small droplets ca. 2 weeks before drying, 2–3 days before first stamens emerge; lateral stamens emerging simultaneously on all flowers, soon followed by third and fourth stamens, exserted on long, whitish filaments, 0.3–1 mm long, 0.2–0.3 mm wide, which slowly retract holding anthers in a tight circle around and above pistil; anthers pale yellow, 0.3–0.4 mm long, 0.5–0.6 mm wide; thecae ellipsoid; pollen pale yellow fading to white. INFRUCTESCENCE with spadix 5–11 cm long; berries obovoid, greenish-yellow to white, 4–4.3 mm long, 2.5 mm thick, sharply pointed at apex; seeds 2. Fig. 63.

Anthurium cuneatissimum is known from the Atlantic slopes in Costa Rica and Panama in tropical wet forest life zones from 20 to 450 m elevation in Costa Rica and at much higher elevations of 800 to 1,000 m in Panama.

The species is in section *Pachyneurium* and is distinguished by its long, usually quadrangular, sharply margined petiole, broad leaf blade, cupulate, coriaceous, ovate spathe, short clavate, lemon-yellow spadix, and white obovoid berries. It is confused only with *A. spathiphyllum*, which shares a similar short clavate, sometimes yellowish spadix. That species differs, however, in having much narrower leaves with 20–30 prominently sunken primary lateral veins (versus (5)10–15 scarcely sunken veins for *A. cuneatissimum*), commonly 3-sided petioles, and a spathe that is lanceolate to broadly lanceolate and about twice as long as the spadix (versus ovate and about as long as the spadix for *A. cuneatissimum*).

This species was not distinguished in the treatment of the genus *Anthurium* for Costa Rica (Croat & Baker, 1979) even though we initially had material separated along these lines before finding that the 3-sided versus 4-sided petiole character breaks down. Special thanks go to Michael H. Grayum (University of Massachusetts) for pointing out additional characters that made their separation possible.

COSTA RICA. ALAJUELA: NNE of Bijagua, *Burger & Baker 9820* (MO); *Croat 36275*; *36296*; *36454*; *36480A* (MO). HEREDIA: near Puerto Viejo along road near Río Sucio, *Croat 35751* (MO).

Anthurium cuspidatum Mast., Gard. Chron. 3: 428. 1875. TYPE: Colombia? Hort. Vietch., January 1875 (K).

Anthurium talamancae Engl., Bot. Jahrb. Syst. 25: 386. 1898. TYPE: Costa Rica. Limón: Talamanca, near Shirores, 100 m, *Tonduz 9233* (B, hololectotype, designated Croat & Baker, 1979).

Anthurium donnellsmithii Engl., Bot. Jahrb. Syst. 25: 389. 1898. TYPE: Costa Rica. Limón: Río Jiménez, Llanos de Santa Clara, 280 m, April 1894, *J Donnell Smith 4979* (B, holotype; US, isotype).

Anthurium orteganum Engl., Bot. Jahrb. Syst. 25: 387. 1898. TYPE: Colombia. Cauca: near Popoyán, 1,500–1,700 m, *Lehmann 5989* (B, holotype; F, K, isotypes).

Anthurium johnii Engl., Pflanzenr. IV 23B: 119. 1905. TYPE: Costa Rica. Limón: Suerre, Llanos de Santa Clara, 300 m, *J Donnell Smith 6812* (B).

Epiphyte or terrestrial; stems often to 50 cm long, ca. 3 cm diam.; internodes short; cataphylls 7–15 cm long, subcoriaceous, drying pale reddish-brown, weathering into fibers. LEAVES erect-spreading; petioles terete, 30–118 cm long, 4–12 mm diam.; geniculum 2–3 cm long; blades usually ovate-oblong, sometimes narrowly ovate, moderately chartaceous, abruptly acuminate at apex, truncate to subcordate to rarely prominently lobed at base, 25–62 cm long, 11–40 cm wide; the sinus (when blade is lobed) hippocrepiform to spathulate; midrib convexly raised above and below; primary lateral veins 11–15 per side, sunken above, raised below, often reddish beneath; lesser veins sunken above, raised below; collective vein arising from one of the lowermost basal veins, sunken above, raised below, 1–2 mm from margin. INFLORESCENCE erect-spreading, shorter than or equal to the leaves; peduncle 28–46 cm long, terete; spathe membranaceous,

oblong-lanceolate, pale green, sometimes tinged purple, 7.5–18 cm long, 1.8–2.5 cm wide, gradually acuminate at apex, round at base; spadix green to usually dark violet-purple, 6.5–18 cm long, ca. 5.5 mm diam. at base, 4.5 mm diam. at apex; flowers rhombic, 3.5–3.8 mm long, 2.8–3 mm wide, the sides straight to weakly sigmoid; 4–5 flowers visible in the principal spiral, 5–6 flowers visible in the alternate spiral; tepals glossy; pistils weakly emergent, violet-purple; stigma linear, ca. 0.5 mm long; stamens emerging in scattered manner from base, the basal one quarter of spadix with 4 stamens before those in the apical one half emerge, held in tight contiguous cluster obscuring pistil; anthers violet-purple; thecae oblong, scarcely divaricate; pollen pale purple fading to white. INFRUCTESCENCE pendent; spadix to 27 cm long; berries purple-violet to reddish-violet, ovoid-ellipsoid, 6–8 mm long, ca. 5.3 mm wide. Figs. 64 and 65.

The species is found from Nicaragua to Ecuador at elevations from 400 to 1,700 m or rarely lower in very wet areas, in premontane wet, tropical wet, premontane rain, and lower montane rain forest life zones. It is one of the more common species of *Anthurium.*

Anthurium cuspidatum is distinguished by its thin, usually oblong-ovate blades with many veins (these often drying reddish-brown or with purplish splotches on the blade) and by its long, slender, weakly tapered, violet-purple spadix and early exserted, oblong berries that are exserted a long time before they ultimately ripen red. An unusual feature not previously seen on any other *Anthurium* is exhibited by *Croat 25605.* In that specimen the uppermost roots were subtended by and enveloped in cataphylls.

Anthurium cuspidatum was placed in section *Polyneurium* by Engler but has since been shown to be an atypical member of section *Pachyneurium* because of its involute vernation. It is superficially close to *A. williamsii* of Costa Rica, Panama, and northwestern South America, with which it shares a nearly identical inflorescence and similar thin, veiny leaves. *Anthurium williamsii,* in section *Polyneurium,* differs in having supervolute vernation and a more ovate blade with more basal veins that are free or nearly free to the base. *Anthurium cuspidatum* is quite variable in leaf shape with blades sometimes ovate, similar to *A. williamsii,* but when this is the case, *A. cuspidatum* can be distinquished by having a definite posterior rib (coalesced basal veins).

Anthurium cuspidatum has a number of sibling species in the coastal and sub-Andean portions of Colombia and Ecuador. Many of these species may prove to be synonymous but others have radically different inflorescences while sharing similar leaf blades with numerous primary lateral veins. Included in the complex are *A. monticolum* Engl., *A. longicaudatum* Engl., *A. oreophilum* Sodiro, and others.

COSTA RICA. ALAJUELA: NNE of Bijagua, *Croat 36258, 36312* (MO); road from Cariblanco to Lake Hule, *Baker et al. 224* (F, MO); Finca Los Ensayos, NW of Zarcero, *Croat 43590* (MO); E rim of Lake Hule, *Luteyn 3353* (MO); between Naranjo and Aguas Zarcas, *Croat 46958* (MO); N of Río Naranjo along road to Upala, *Utley & Utley 5343* (DUKE); San Carlos, *Smith 1658* (MO); between Volcán Poás and Volcán Barba, *Croat 35466* (MO). CARTAGO: road between Juan Vinas and Turrialba, *Croat 36830* (MO); road between Moravia to Quebrada Platanillo, *Croat 36653, 36673* (MO); along Río Grande de Orosi between bridge and Tapantaí, *Gentry 976* (MO); between Trinidad and Colblanco, *Utley & Utley 2724* (MO). HEREDIA: vicinity Bajo La Hondura, *Croat 44511* (MO); S of Cariblanco, *Croat 35776* (MO); near Puerto Viejo, along road near Río Sucio, *Croat 35694, 35763* (MO); near Río Pará Blanco, *Lent 2856* (MO); N of Vara Blanca, *Croat 35607* (MO). LIMÓN: Hacienda Tapezco-Hacienda La Suerte, W of Tortuguero, *Davidson 6746, 6991* (MO); between Siguerres and Limón, *Baker 185* (F, MO); *Burger et al. 10522* (F, MO); SW of Siguerres, *Utley & Utley 5445* (DUKE); Talamanca, *Pittier & Tonduz 9233* (BR, US); between Turrialba and Limón, *Croat 43307* (MO). SAN JOSÉ: slopes above Alfombra along road from San Isidro del General to Dominical, *Burger & Baker 10094* (F, MO); *Burger & Visconti 10677* (F, MO); Bajo La Hondura, *Utley & Utley 4997* (DUKE, MO); between Río Cascajal and Río Hondura, *Lent 3785* (MO); between San Isidro del General and Dominical, *Croat 35321* (MO).

NICARAGUA. MATAGALPA: Cerro Musún, *Neill 1815* (MO). RÍO SAN JUAN: near Caño Chontaleño, NE of El Castillo, *Neill 3426* (MO).

Anthurium davidsoniae Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 4. 1940. TYPE: Panama. Chiriquí: Bajo Chorro, Boquete District, 1,800 m, 17 January 1938, *M. E. Davidson 134* (F 915728, holotype; MO, US, isotype).

Usually terrestrial, rarely epiphytic; stems elongate, less than 1 cm diam.; internodes short at apex, longer in lower portion of stem; cataphylls moderately thick, to 12 cm long, drying reddish-brown. LEAVES ± erect; petioles shallowly sulcate with sharp marginal ribs adaxially.

13–27 cm long, 2.5–3.5 mm wide; blades ovate to narrowly ovate, ± chartaceous, usually conspicuously bullate, 15–23 cm long, 9.5–15.5 cm wide, long-acuminate at apex, shallowly and broadly lobed at base; the upper surface pale green, the lower surface slightly paler; the midrib narrowly raised; primary lateral veins 10–12 per side, sunken, straight or weakly arched to collective vein; collective vein arising from the first or second basal vein, 6–8 mm from margin. INFLORESCENCE erect, shorter than leaves; peduncle 9–19 cm long; spathe lanceolate, pale green, 3–5 cm long, 5–10 mm wide; spadix pale yellow-green, 2–4 cm long, 5–7 mm diam. at base, 2–3 mm diam. at apex; flowers rhombic to 4-lobed, 2.3–2.7 mm long, 2.7–3 mm wide; 3–5 flowers visible in the principal spiral, 4–7 flowers visible in the alternate spiral; tepals matte, lateral tepals 1–1.2 mm wide; pistil emergent, green; stigmas exserted, brushlike; stamens emerging but may retract (not evident on dry specimens). INFRUCTESCENCE with spadix 3.5–6 cm long; berries greenish-yellow; mesocarp syrupy; seeds obovoid, yellow-green, darker at apex with numerous raphide cells visible on the surface. Fig. 70.

Anthurium davidsoniae is known from Costa Rica and western Panama, from 1,300 to 2,000 m elevation in premontane rain and lower montane rain forest.

The species is related to both *A. pallens* and *A. microspadix*, although more closely to the latter. All of these species share a similar habit with elongate stems and a similar inflorescence. *Anthurium davidsoniae* differs from both others by having a much broader, more ovate, more conspicuously bullate leaf blade.

All three of the above species occur in similar cloud forest habitats and evaluation of herbarium material alone is unsatisfactory in separation considering the variability of *Anthurium*. Field observations have convinced me, however, that they are all good species. *Anthurium davidsoniae* and *A. microspadix* are both semi-erect plants and are usually terrestrial but require something to lean on for support. *Anthurium pallens* is usually a pendent epiphyte. *Anthurium davidsoniae* is placed in section *Xialophyllium* in an alliance I refer to as the *A. microspadix* alliance. This group, which differs substantially from other members of section *Xialophyllium* such as *A. caucanum* Engl., may ultimately have to be considered a separate section. All species in the group share thin, prominently veined, often bullate leaves, elongate slender stems, and commonly green inflorescences and fruits.

COSTA RICA. ALAJUELA: no other location, *Smith 1123* (NY); Zarcero, *Smith 431* (MO). CARTAGO: vicinity Orosí, *Standley 39928* (US); S of Tapantí, *Burger & Burger 8434* (F, MO, U). GUANACASTE: no other location, *Primack et al. 433* (DUKE). HEREDIA: N of Vara Blanca, *Croat 36023* (MO); *Skutch 3644* (MICH, MO, NY). PUNTARENAS & ALAJUELA: Monteverde reserve, *Burger & Baker 9734* (F, MO). SAN JOSÉ & HEREDIA: Cerro Zurquí, *Almeda 3687* (CAS). SAN JOSÉ: NW of Cascajal, *Taylor 11303* (NY).

Anthurium durandii Engl., Bot. Jahrb. Syst. 25: 401. 1898. TYPE: Costa Rica. Inter la Division et l'Alto del Palmital, January 1891, *Pittier 3868* (B, hololectotype; BR, CR, isolectotypes, designated Croat & Baker, 1979).

Anthurium littorale Engl., Bot. Jahrb. Syst. 25: 405. 1898. TYPE: Costa Rica. Marais de Sierpe, March 1892, *Pittier 6837* (BR, holotype; CR, isotype).

Epiphytic or rarely terrestrial; stems short; internodes sometimes to 3 cm long; roots short, sometimes purplish; cataphylls moderately thin, 5.4–6 cm long acuminate at apex, drying pale brown, weathering to reticulate fibers, ultimately deciduous. LEAVES erect-spreading; petioles 9–25 cm long, 4–5 mm diam., broadly and sharply sulcate adaxially, rounded abaxially, sparsely, dark glandular-punctate; geniculum 1.5–3 cm long; blades elliptic, coriaceous, short-acuminate at apex, obtuse at base, 10–31 cm long, 4–15 cm wide, broadest near middle; both surfaces matte, dark glandular-punctate, the lower surface paler, the upper surface drying with an alveolate pattern; midrib convexly raised at base above, acute at middle, weakly sunken toward apex, convexly raised below, narrowing toward apex; primary lateral veins 8–15 per side, departing midrib at 45° angle, straight to collective vein, flat to weakly sunken above, raised below, lesser veins obscure; collective vein arising from the base, 9–15 mm from the margin, a secondary collective vein sometimes extending to about the middle of the blade. INFLORESCENCE spreading, shorter than or equalling leaves; peduncle 12–40 cm long, ca. 3 mm diam.; spathe moderately thin, pale green to pinkish green (B & K Yellow-green 7/7.5), oblong-lanceolate, 4–7 cm long, 1–1.5 cm wide, broadest near the base, abruptly acuminate at apex, acute at base, inserted at ca.

FIGURES 66–69. — 66. *Anthurium durandii* Engl., *Fennell s.n.* — 67. *Anthurium eximium* Engl., *Orchid Jungle 4-80.* — 68. *Anthurium eximium* Engl., *Las Cruces Bot. Gard.* — 69. *Anthurium flexile* Schott, *Croat 40285.*

FIGURES 70–73. 70. *Anthurium davidsoniae* Standl., *Croat 48592*.—71–72. *Anthurium fatoense* K. Krause, *Folsom 2949*.—73. *Anthurium flexile* Schott, *Croat 36467*.

65° angle on peduncle; spadix pale green turning reddish brown, narrowly tapered toward apex, 10–16.5 cm long, 4–9 mm diam. at base, 2–4 mm diam. at apex; flowers 4-lobed, 3–4 mm long, 2.5–3 mm wide, the sides straight in the direction of the principal spiral, sigmoid perpendicular to the spiral; ca. 3 flowers visible in the principal spiral, ca. 5 flowers visible in the alternate spiral; tepals semiglossy, lateral tepals 1.8–2.2 mm wide, the inner margin convex; pistils emergent but not raised, square, green; stigmas scarcely visible, ca. 0.2 mm long, drying black; stamens emerging from the base, laterals first, scarcely exposed, quickly retracting before alternates emerge; pollen white. INFRUCTESCENCE with spadix to 22 cm long; berries ovoid, probably orange. Fig. 66.

Anthurium durandii is known only from Costa Rica on the Pacific slope in San José and Puntarenas Province at elevations from near sea level to 1,600 m in tropical wet and premontane rain forest.

It was initially confused with *A. paludosum* by Standley, which was reported from the Atlantic slope of Costa Rica. *Anthurium durandii* resembles *A. paludosum* superficially but differs in having the cataphyll weathering into a dense fibrous network and in having longer petioles, one third to equally as long as the blade and in having a more or less elliptic leaf blade. It is a member of section *Porphyrochitonium*.

Engler cited two specimens in his original description of *A. durandii*. The second of these, *Tonduz 8422* (BR) is *A. gracile* (Rudge) Lindl.

COSTA RICA. No other location, *Pittier 3868, 6837* (BR). PUNTARENAS: Finca Loma Linda, SW of Cañas Gordas, *Liesner 645* (NY, US); *231* (MO, NY, US); along Fila Las Cruces, *Luteyn 3855* (DUKE); Osa Peninsula, W of Rincon de Osa, *Burger & Liesner 7322* (MO); *Liesner 1845* (MO); *Raven 21510* (DS); S of San Vito de Java, *Raven 21758, 21841* (DS). SAN JOSÉ: below Santa Maria de Doto, *Croat 55203* (MO).

Anthurium eximium Engl., Bot. Jahrb. Syst. 25: 412. 1898. TYPE: Costa Rica. Puntarenas: in forest near Punta Mala, *Tonduz 6768* (BR, hololectotype (two sheets); CR, isolectotype; designated Croat & Baker, 1979).

Epiphyte; stem elongate, ca. 1 cm diam.; roots thick; cataphylls persisting intact, overlapping at base, drying yellow-brown. LEAVES spreading; petioles broadly sulcate, rounded to 3-ribbed abaxially, 7–12 cm long, 6–7 mm diam.; blades narrowly oblanceolate, subcoriaceous, 40–80 cm long, 5–11.5 cm wide, narrowly attenuate at base, long-acuminate at apex; primary lateral veins 10–12 per side, raised above and below (dry), departing midrib at 40°–45° angle, weakly arched to collective vein; the collective vein arising from the base or one of the lowermost primary lateral veins, 1–4 mm from margin. INFLORESCENCE shorter than leaves; peduncle 29–32 cm long; spathe lanceolate-ovate, green, 5–7.7 cm long, 2–2.6 cm wide, clasping at base; spadix creamy white, oblong to clavate, 4.5–6 cm long, 0.8–1 cm diam. at base, 9 mm diam. at apex; 10–12 flowers visible in the principal spiral; tepals matte, longer than wide; stamens exserted, emerging in a somewhat irregular fashion in a complete sequence, the leading stamens 1–2 spirals ahead of the third and fourth; pollen yellow, faintly aromatic at anthesis. INFRUCTESCENCE with spadix to 13 cm long; 1.5–1.7 cm diam.; berries bright red, obovoid, ca. 4.6–7 mm long, 4–5 mm wide; seeds 2, 2.7–2.9 mm long, 1.5–1.7 mm wide. Figs. 67 and 68.

The species is found in Costa Rica in tropical wet forest formations from sea level to 800 m elevation. Until recently it was known only from the Osa Peninsula and the adjacent Golfo Dulce region, but now it has been collected in San José Province on the road to Purrita.

Anthurium eximium can be distinguished by the oblanceolate, epunctate leaves, the persisting cataphylls, the clasping, lanceolate spathe, the cylindrical to clavate spadix, and the bright red berries. The species resembles *A. spathiphyllum*, which is restricted to the Atlantic slope, in spadix and leaf characters, but can be distinguished by the persisting cataphylls.

In his monograph, Engler (1905) cited *A. eximium* as a synonym of *A. consobrinum*. The leaf shapes in both species are very similar. However, Schott's illustration of *A. consobrinum* clearly shows a long, slightly tapering spadix with pistils and berries greatly exceeding the tepals. *Anthurium consobrinum* is a common species of the Atlantic lowlands and numerous collections are consistent with Schott's drawing. The berries of *A. consobrinum* are white with purple, pink or orange apices as opposed to the solid bright red berries of *A. eximium*. In addition, the pistils of *A. consobrinum* are early long-exserted and are held at about the level of the stamens at anthesis.

Anthurium eximium is a member of section *Pachyneurium* despite certain features it shares with section *Calomystrium*, including the thick.

persistent, intact cataphylls and the presence of linear raphide cells on both blade surfaces.

COSTA RICA. No other location, *Pittier 6768* (BR). PUNTARENAS: Osa Peninsula, Corcovado National Park, *Liesner 2846, 2996* (MO); above Palmar Norte, *Croat 35121* (MO); Punta Mala, *Tonduz 6768* (BR); Rincón de Osa, *Burger & Liesner 7286* (MO, NY); *Liesner 1934* (MO); Santo Domingo of Golfo Dulce, *Tonduz 7260* (BR, CR, US). SAN JOSÉ: below Santa Maria de Doto, *Croat 55204* (MO).

Anthurium fatoense K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11: 611. 1932. TYPE: Panama. Colón: Dos Bocas, Río Fato Valley, 40–80 m elev., *Pittier 4227* (US).

Rosulate epiphyte; stems to 60 cm long, usually much shorter, ca. 1 cm diam.; dense mass of greenish roots, acute and ascending at tips; cataphylls subcoriaceous, sometimes tinged with red, 5–10 cm long, drying medium brown, persisting ± intact. LEAVES erect-spreading; petioles quadrangular, sulcate, 2.5–5(9.5) cm long, 5–7 mm wide; geniculum 7–10(20) mm long; blades oblong-oblanceolate, gradually acuminate at apex, acute at base, 24–83 cm long, 6–26 cm wide, broadest at middle or above; both surfaces semiglossy; midrib acutely raised above, square and prominently raised below; primary lateral veins 8–16 per side, departing midrib at 45° angle, arcuate-ascending, acutely raised above, raised and sometimes reddish below; submarginal collective vein arising in the apical quarter of blade, 2–9 mm from margin. INFLORESCENCE erect-spreading to arching-pendent, shorter than or equalling leaves; peduncle 14–48 cm long, subterete, faintly ribbed; spathe pale green, sometimes tinged purplish, narrowly lanceolate, 5.5–9 cm long, 0.7–1.3 cm wide, narrowly long-acuminate to abruptly acuminate at apex, obtuse to subcordate at base; spadix pale reddish or green tinged reddish, 5–15 cm long, 4–8 mm diam. at base, 2.5–4 mm diam. at apex; flowers rhombic to weakly 4-lobed, 1.8–2.8 mm long, 2–3 mm wide, the sides straight parallel to principal spiral, gradually sigmoid on alternate sides; 5–9 flowers visible in the principal spiral and 5–12 flowers visible in the alternate spiral; tepals matte to weakly glossy, lateral tepals 1.2–1.5 mm wide, the inner margins straight to broadly rounded; pistils emergent 1–6 mm, pale green or white: stigma brushlike, ca. 0.5 mm long; stamens emerging in a slow progression from the base in a ± complete sequence, well exserted and held against sides of exserted pistils; anthers white, 0.5–0.6 mm long, 0.5–0.8 mm wide; thecae broadly ovate; pollen white. INFRUCTESCENCE with spadix to 26 cm long; berries cream to greenish-yellow or orange, oblong-ovoid, 4–7 mm long, acute at apex. Figs. 71 and 72.

The species is known from southern Costa Rica and Panama, occurring principally on the Caribbean slope from sea level to 1,000 m in wetter parts of tropical moist forest as well as in tropical wet, premontane wet and lower montane wet forest. It also occurs on the Pacific slope in the Fortuna area of Chiriquí Province.

Anthurium fatoense is a member of section *Pachyneurium* and is considerably variable in the size of the leaves and inflorescences as well as in berry color. It is most easily confused with *A. consobrinum* in Costa Rica and is distinguished by its tapered, greenish spadix, which has the stamens emerged in a close cluster with the pistil not at all apparent. In the flowers of *A. consobrinum,* the pistil emerges well ahead of the stamens and dwarfs the stamens in size, extending several millimeters above the stamens. Despite the close vegetative resemblance of the two species, they are probably not closely related.

COSTA RICA. ALAJUELA: between Naranjo & Aguas Zarcas, NE of Villa Quesada, *Croat 46976* (MO). LIMÓN: S of Punta Cahuita, *Croat 43197* (MO); between Río Bananito & Cahuita, *Burger et al. 10485* (MO).

Anthurium flexile Schott, Oesterr. Bot. Z. 8: 180. 1858.

a. Anthurium flexile ssp. **flexile.** TYPE: Costa Rica. Heredia: Pedregel, *Wendland 932* (GOET, holotype).

Anthurium myosuroides (H.B.K.) Endl. var. *angustifolia* Engl., Bot. Jahrb. Syst. 25: 382. 1898. TYPE: Costa Rica. Limón: Matina, *Pittier 9797* (*Pittier 9767*?) (BR, CR, US).

Scandent epiphyte; the stem elongate; internodes 2–6 cm long, ca. 3 mm thick; roots slender, 1–2 cm long, scattered along the internodes; cataphylls to 4 cm long. LEAVES spreading; petioles 4–11 cm long, flattened to sulcate adaxially; blade elliptic or narrowly elliptic, (10)13–26.5 cm long, (2.5)3–9(10.5) cm wide, acuminate to long-acuminate at apex, narrowly subcordate, pliveined at base, the upper surface semiglossy; midrib sunken; collective vein arising from the base or fused with the midrib for 0.2–2.5 cm from base. INFLORESCENCE usually arching-pendent; penduncle 4–23 cm long, terete; spathe green,

lanceolate, 3.5–9.5 cm long, 0.7–1.8 cm wide; stipe absent or to 2 mm long; spadix violet-purple at anthesis, 4.5–13 cm long, 0.3–0.5 cm diam. at base, usually less than 1 cm diam. at apex. INFRUCTESCENCE with spadix to 2 cm diam.; berries oblong-ellipsoid to narrowly ellipsoid or narrowly ovoid (with four longitudinal ridges on drying), orange to red, 0.5–1.2 cm long, with numerous round to slightly elongated raphide cells visible on drying; mesocarp orange, pulpy; seeds (1)2(3), black, suborbicular, flattened, ca. 6–9 mm long. Figs. 69, 73, and 75.

Anthurium flexile is a member of section *Polyphyllium* and consists of two subspecies. The ssp. *flexile* ranges from Mexico to Panama at 0 to 1,000 m elevation in tropical wet forest life zones. It is distinquished from ssp. *muelleri* by the characters listed in the Key. For a discussion of these differences see the discussion of ssp. *muelleri*.

BELIZE. CAYO DISTRICT: Maya Mountains, Cockscomb, *Schipp S-192* (MICH, MO). STANN CREEK DISTRICT: Sittee River, Kendal, *Schipp 192* (F, NY). TOLEDO DISTRICT: Colombia Forest Station, *Proctor 36087* (MO); Maya Mountains, Gabriel Camp, *Boutin & Schlosser 5153* (MO); near Monkey River, *Gentle 3852* (MO, NY); Río Blanco branch, *Stevenson 110* (F).

COSTA RICA. ALAJUELA: vicinity of Bijagua, *Burger & Baker 9871* (F); *Croat 36467* (MO); Llanura de San Carlos, *Molina et al. 17658* (EAP, F). GUANACASTE: vicinity of Tilarán, *Gentry 2025* (MO); *Standley & Valerio 44253, 44290, 45020, 45997, 46112* (US). HEREDIA: Pedregal, *Wendland 932* (GOET). LIMÓN: Los Diamantes, *Schubert 1133* (US); Matina, *Pittier 9767* (CR, US). PUNTARENAS: SE of the Río Claro, *Burger & Matta 4803* (F). SAN JOSÉ: Tucurrique, *Tonduz 12750* (US).

GUATEMALA. IZABAL: Río Chacón Machaca, *Johnson 1257* (UCLA); Cerro San Gil, along Río Bonito, *Steyermark 41693* (F); *41886* (F, NY). SAN MARCOS: vicinity Finca Armenia, above África, *Croat 40954* (MO). SUCHITEPÉQUEZ: no other location, *Lind 73* (WIS).

HONDURAS. ATLANTIDA: near Point Triunfo, *Wilson 439* (NY); vicinity La Ceiba, *Yuncker et al. 8202* (F, MICH, MO, NY, US); Lancetilla Valley, *Chickering 206* (MICH); *Croat 42654* (MO); *Molina 10454* (EAP, F); *Standley 53105, 53349* (F, US); *56544* (F); *Yuncker 4615* (F, MO). GRACIAS A DIOS: Mosquitia Region, Río Plátano, *Gentry et al. 7518* (MO).

MEXICO. CHIAPAS: vicinity Nuevo Amatenango, *Matuda 30187* (MEXU); vicinity of Munic. Palenque, *Breedlove 24248, 26513, 28889, 35342* (CAS, DS); *34994* (DS); vicinity of Palenque, *Croat 40285* (MO); *Hoover 135* (MO); *Matuda 3644* (MEXU); N of Pichucalco, *Miranda 6628* (MEXU); between Ranchería Coamapa & Campamento San Joaquín, *Gilly & Hernandez 169* (MEXU). TABASCO: vicinity Cerro de Azufre, *Gilly & Hernandez 277, 289* (MEXU); E of Teapa, *Conrad et al. 2881* (MO); *Croat 40129* (MO); Zunú, vicinity Tapijulapa, *Magaña 3127* (MO). VERACRUZ: no other location, *Rosas 1055* (XAL); Biological Station at Tuxtla, *Calderon 2186* (F, XAL); *Goméz-Pompa 4565* (F); *Rosas & Villalpando 1408* (XAL); vicinity Lake Catemaco, *Beaman 5304* (F, MEXU); *Moore 6253* (BH); Cerro de San Martín, *Calzada 577* (F, XAL); vicinity Hidalgotitlán, *Dorantes 2529* (XAL, MEXU); *Goméz-Pompa & Nevling 5185* (XAL); *Vazquez 854* (XAL); NW of La Palma, *Toledo 4* (MEXU); Río Solosúchil, *Vazquez 1625* (XAL).

NICARAGUA. No other location, *Tate 405* (B). MATAGALPA: Cerro Musún, *Neill 1726* (MO). RIVAS: Isla de Ometepe, NW slope of Volcán Maderas, *Stevens 6614* (MO). ZELAYA: along Caño Majagua, *Stevens 6975* (MO); S slopes of Cerro El Inocente, *Stevens 6790* (MO); trail from Cerro Saslaya to San José del Hormiguero, *Stevens 7089* (MO); S of bridge at Colonia Agrícola Yolaina, *Stevens 6466* (MO); *Vincelli 212* (MO); W of Río Wawa ferry on road from Puerto Cabezas, *Stevens 8650* (MO); near Río Okanwás, E of Rosita, *Neill 4428* (MO); vicinity Waní including Río Ulí, *Stevens 7252* (MO).

b. Anthurium flexile ssp. **muelleri** (Macbr.) Croat & Baker, Selbyana 2: 236. 1978. *Anthurium muelleri* Macbr., Candollea 5: 348. 1934. *Anthurium mexicanum* Engl., Monogr. Phan. 2: 105. 1879, non Liebm., 1849. TYPE: Mexico. Veracruz: Orizaba, *Mueller 993* (NY, hololectotype; BR, LE, isolectotypes, here designated).

Anthurium flexile ssp. *muelleri* differs from the typical subspecies in that the leaves are lanceolate, broadest below the middle, weakly cordate at the base and the first pair of basal veins are not fused with the midrib or very rarely so. The spadix may be stipitate 1–1.5 cm. Fig. 74. It occurs in Mexico and Guatemala at elevations of 1,000 to 1,700 m and is replaced by the typical subspecies in southern Central America.

MEXICO. No other location, *Linden 136* (BR). CHIAPAS: Pueblo Nuevo Solistahuacán, *Clark 289* (DS); vicinity of Rayón, Selva Negra, *Breedlove 26132* (CAS, DS). VERACRUZ: Cerro de San Martín, *Calzada 207* (F); Orizaba, *Mueller & Schlumberger 993* (F, US, (Photo)); Santa Marta, Los Tuxtla, *Sousa 3586* (MEXU); San Andrés Tuxtla, *Beaman & Alvarez 5349* (F, MEXU); *Sousa 3445* (CAS, MEXU).

GUATEMALA. CHIMALTENANGO: Panajabal, *Standley 62281* (F); *62121* (F); near Sibajá, *Standley 62281* (F). QUEZALTENANGO: between Finca Pirineos and Patzulín, *Standley 86955, 86977, 86990* (F); along Quebrada San Jerónimo, Finca Pirineos, vicinity Santa María de Jesús, *Steyermark 33336, 33450* (F); *Standley 68324, 84858* (F). SAN MARCOS: La Trinidad, *Croat 40875* (MO); above Finca El Porvenir, *Standley 37414* (F); *Steyermark 37212, 37240* (F). SOLALÁ: Volcán Atitlán, above Finca Mocá, *Steyermark 47925* (F, MO).

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FIGURE 74. *Anthurium flexile* ssp. *muelleri* (Macbr.) Croat & Baker. *Molina et al. 17658.*

FIGURES 75–78. 75. *Anthurium flexile* Schott, *Croat 36467*.—76. *Anthurium formosum* Schott, *Croat 35775*.—77. *Anthurium gracile* (Rudge) Lindl., *Croat 38191*.—78. *Anthurium hacumense* Engl. (Cultivated Climatron MBG.)

Anthurium formosum Schott, Oesterr. Bot. Z. 8: 181. 1858. TYPE: Costa Rica. Cartago?: near Naranjo, *Wendland 583* (GOET).

Anthurium lactiflorum Engl., Bot. Jahrb. Syst. 6: 277. 1885. TYPE: Colombia, *Lehmann 2582* (B).

Epiphytic or often terrestrial; stems often to 1 m long; roots thick, directed downward; cataphylls coriaceous, narrowly rounded at apex, with subapical apiculum, drying tan, persisting intact. LEAVES erect-spreading; petioles 40–150 cm long, 0.6–1 cm diam., subterete, weakly flattened or weakly sulcate adaxially; geniculum 2–2.2 cm long, tinged pinkish; blades ovate, 30–80 cm long, 20–52 cm wide, acuminate and turning down at apex, deeply lobed at base; anterior lobe 31–54 cm long; the posterior lobes 13–20 cm long; sinus broadly hippocrepiform to spathulate; both surfaces glossy; midrib acutely raised above and below; primary lateral veins 7–9 per side, sunken in valleys above, raised below; interprimary veins sunken above, raised below; basal veins 7–8 pairs, the fourth to sixth coalesced 2.5–3 cm; the posterior rib naked, turned up; collective vein usually arising from one of the lowermost basal veins, frequently from the second or third basal vein, 2–4 mm from the margin. INFLORESCENCE erect-spreading; peduncle 21–47 cm long, stout; spathe subcoriaceous, ovate or oblong-elliptic, pale greenish white to pale violet, 12.5–24 cm long, 3–8.5 cm wide, cuspidate at apex, round at base, held close to spadix even in fruit, inserted at 45° angle on peduncle; spadix stipitate 12–15 mm in front, 2–3 mm in back, white to violet-purple, ± oblong to tapered to both ends, 5.5–14.5 cm long, 1.2–1.5 cm diam. at middle, 7–9 mm at base and apex; flowers rhombic to 4-lobed, 2.3–3 mm long, 3–3.8 mm wide, the sides jaggedly sigmoid; 9–15 flowers visible in the principal spiral, 10–20 flowers visible in the alternate spiral; tepals glossy, the lateral tepals 1–1.5 mm wide, the inner margins rounded to angulate; pistils early emergent; stigmas deep purple, ultimately brushlike; stamens emerging from base of spadix, the lateral stamens emerging throughout before alternate stamens emerge, held in a tight cluster over pistil; filaments pale lavender; anthers pale lavender to deep red-violet, sometimes white tinged with red-violet at margins; pollen white. INFRUCTESCENCE with spadix 18–32 cm long; berries dark reddish-violet to violet-purple, often reddish-orange at base, narrowly acute at apex, 10–12 mm long, 4–5 mm wide; seeds 2, 7–8.4 mm long, 3–3.5 mm wide. Figs. 76 and 79.

The species is found in Costa Rica, Panama, Colombia, and perhaps also Ecuador [see *Gentry 9621* (MO)] at elevations of 500 to 1,500 m. In Costa Rica and Panama the species occurs in premontane wet forest and more commonly in premontane rain forest and lower montane rain forest. It is often one of the most common species at middle elevations, where it is generally found along shady road banks and sometimes forms large stands.

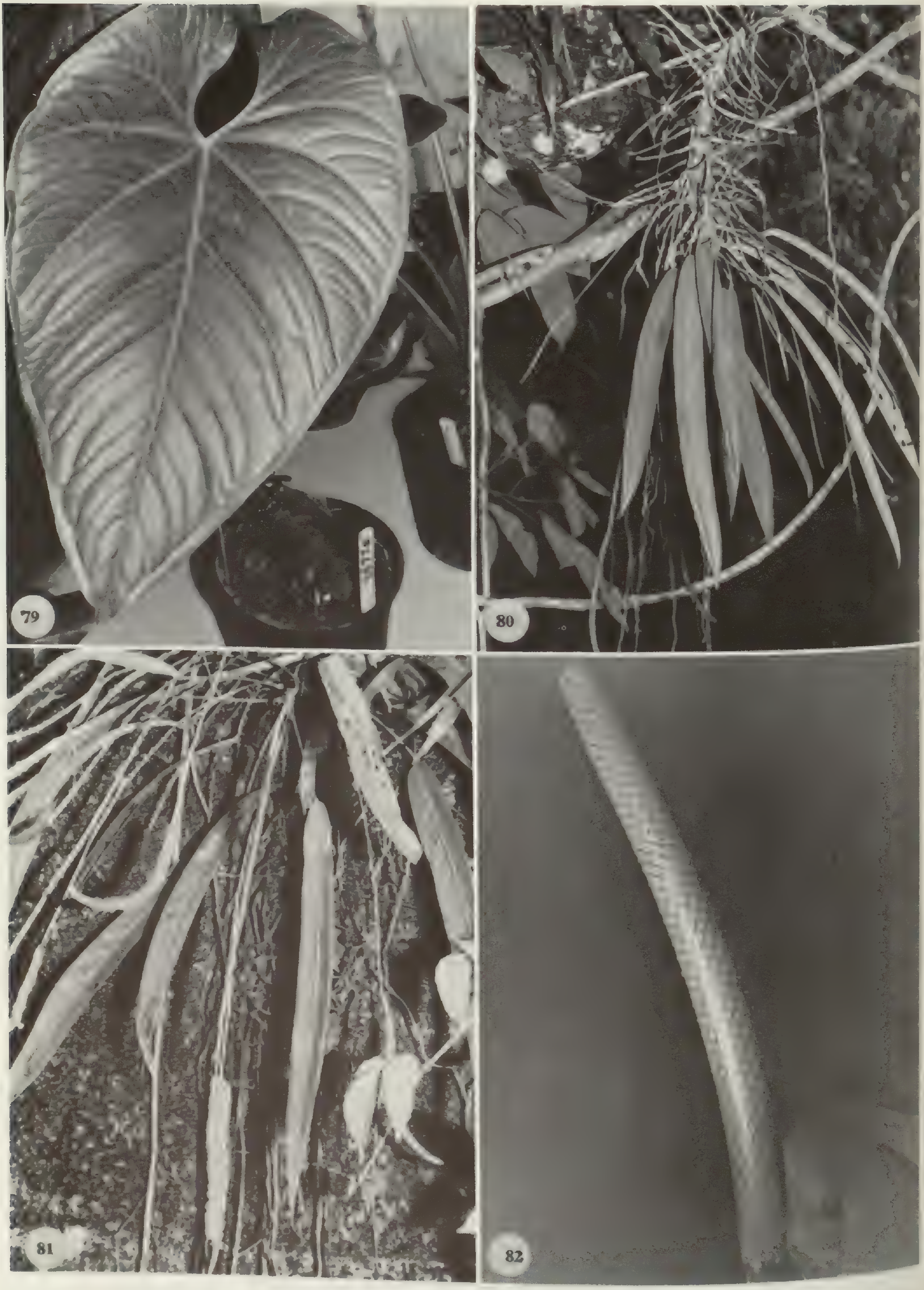
Anthurium formosum is variable both in size of leaves and inflorescences and in the color of the spathe and spadix, both of which vary from white to purplish-violet at anthesis. The spathe and spadix, if white at anthesis, tend to become more colored with age. The collective vein is also quite variable, sometimes arising from one of the lowermost basal veins or sometimes from the second or third basal vein.

The species is a member of section *Calomystrium* and is distinguished by its usually large cordate blade with a prominent posterior rib, by its large ovate or oblong-elliptic, subcoriaceous spathe, glossy tepals, sharp, early-emergent pistils and reddish-violet to violet-purple berries. Leaf blades usually dry olive green with characteristic reddish-brown veins and with purplish and/or brownish blotches.

COSTA RICA. CARTAGO: Finca Navarro, *Maxon 647* (NY); between Tuis & Bajo Pacuare along road from Turrialba to Moravia, *Burger et al. 10031* (DUKE, MO); road from Turrialba to Moravia, *Croat 36552, 36571* (MO); road from Moravia to Quebrada Platanillo, *Croat 36680* (MO); SW of Paraiso, *Croat 47051* (MO); SE of Platanillo, *Croat 36716, 36745* (MO); vicinity Platanillo, *Donnell Smith 251, 252* (US); valley of Río Tuis, *Tonduz 8216* (BR); near Narajo, *Wendland 583* (GOET). HEREDIA: S of Cariblanco, *Croat 35775, 35834* (MO); Tirimbina, *Proctor 32286* (LL); N of Vara Blanca, *Croat 35567, 35634* (MO); S of Siguirres, *Croat 43308* (MO). PUNTARENAS: Las Cruces Botanical Garden, *Croat 32967* (MO). SAN JOSÉ: vicinity Bajo La Hondura, *Croat 44498, 44519* (MO); *Luteyn 3317* (DUKE, MO); *Utley & Utley, 4995, 4996* (DUKE).

Anthurium friedrichsthalii Schott, Oesterr. Bot. Wochenbl. 5: 65. 1855. *Anthurium gracile* (Rudge) Lindl. var. *friedrichsthalii* (Schott) Engl., Bot. Jahrb. Syst. 25: 370. 1898. TYPE: Guatemala. Insula Cativo, *Friedrichsthal s.n.* (W, Type destroyed; Photo of Schott Aroid Drawing #332, NYBG Neg. #N.S. 3819).

Anthurium linearifolium Engl., Bot. Jahrb. Syst. 25: 370. 1898. TYPE: Panama. Canal Zone: Río Chagres, *Lehmann 4538* (B, K).



FIGURES 79–82. 79. *Anthurium formosum* Schott, *Croat 35775*.—80. *Anthurium friedrichsthalii* Schott, *Croat 14187*.—81. *Anthurium friedrichsthalii* Schott, *Croat 16557*.—82. *Anthurium hacumense* Engl., *Croat 32903*.

Epiphyte, usually pendent, often loosely attached by only a few roots; stem usually less than 15 cm long, 1–1.5 cm diam.; roots thin; cataphylls weathering to coarse linear-fibers. LEAVES pendent; petioles 1.5–14 cm long, mostly less than 10 cm long, ca. 2–3 mm diam., terete or flattened adaxially; geniculum 5–8 mm long; blades linear, 12–56 cm long, 0.8–4 cm wide, acuminate at apex, subacute at base; upper surface matte to semiglossy, the lower surface conspicuously glandular-punctate; the midrib acutely raised, becoming sunken at apex above, convexly raised at base, flattened at apex below; primary lateral veins 8 or more per side, flat above, obscure below; collective vein arising from the base, 3–5 mm from margin. INFLORESCENCE pendent; peduncles 19–30 cm long, ca. 2.5 mm diam., terete; spathe linear, pale green, 1–5 cm long, 3–5 mm wide, rounded at base, gradually acuminate at apex, withering and soon deciduous; spadix pale green, sometimes tinged purplish, turning brownish, 3–15 cm long, 4–5 mm diam.; the flowers 4-lobed, 2.8–3.8 mm in both directions, the sides straight to weakly sigmoid; 3–4 flowers visible in the principal spiral, 2–3 flowers visible in the alternate spiral; tepals matte, minutely papillate, lateral tepals 1.6–2 mm wide; pistil not exserted; the stigma linear, 3 mm long; stamens emerging ± slowly from base, held at edge of pistil, soon completely retracting; anthers cream, ca. 0.3 mm long, 0.9 mm wide; thecae ellipsoid; pollen white. INFRUCTESCENCE pendent; spathe absent; spadix to 25 cm long, 2 cm diam.; berries pale yellow-orange, irregularly shaped broader than long, ca. 5 mm long, 5–8 mm wide, narrowing to apex, truncate with a central depression; seeds 3–4, ± ovate, greenish or yellowish, ca. 2.7 mm long. Figs. 80 and 81.

The species is found from Guatemala to Colombia at elevations from sea level to usually 800 m. In Costa Rica and Panama it is common in tropical moist forest and is also known from premontane wet and tropical wet forest.

Anthurium friedrichsthalii is recognized by its pendent habit and the thick, linear, bicolored, punctate leaves. Juvenile plants have short, elliptic leaves. See the discussion under *A. gracile* for differences with that species. It is a member of section *Porphyrochitonium* differing from the more typical members of that section only in its linear leaves and pendent habit.

COSTA RICA. ALAJUELA: N of San Miguel, *Croat 35650* (MO). CARTAGO: vicinity Santa Teresa, *Luteyn 3249* (DUKE); E of Cachí, *Croat 47085* (MO). HEREDIA: vicinity La Virgin, *Lent 1510* (NY). LIMÓN: Hacienda Tapezco-Hacienda La Suerte, *Davidson 7102, 7104* (LAM). PUNTARENAS: vicinity Monteverde, *Luteyn 3398* (DUKE); *Primack et al. 428* (DUKE); *Wilbur et al. 15822* (DUKE); Rincón de Osa, *Liesner 1809, 1930* (MO). SAN JOSÉ: La Palma, *Luteyn 3308* (DUKE).

Anthurium gracile (Rudge) Lindl., Edward's Bot. Reg. 19: t. 1635. 1833. *Pothos gracilis* Rudge, Pl. Guian. Rar. 23, T. 32. 1805. TYPE: French Guiana, *Martin s.n.* (Herb. Rudge, BM).

Anthurium scolopendrinum (W. Ham.) Kunth, Enum. Pl. 3: 68. 1841. *Pothos scolopendrinus* W. Ham. TYPE: French Guiana, *Desvaux s.n.* (P).
Anthurium longipes Matuda, Bol. Soc. Bot. México 14: 23. 1952, non N. E. Brown, 1882. TYPE: Belize, *Gentle 2624A* (MICH).

Epiphyte, usually erect; roots white; stems 1.5–30 cm long, 7–10 mm diam.; internodes short; cataphylls membranaceous, 2–9.5 cm long, drying reddish or brown, persisting intact, ultimately deciduous. LEAVES ± erect; petioles 1–20 cm long, ca. 3 mm diam., subterete flattened adaxially; the geniculum ca. 5 mm long; blades moderately thin, oblanceolate, 11–32 cm long, 3–8.5 cm wide, acuminate at apex, gradually tapered to long-cuneate at base; the upper surface matte to semiglossy; the midrib prominently raised almost to apex above, raised below; primary lateral veins numerous, nearly obscure; collective vein arising from base, 4–7 mm from margin. INFLORESCENCE ± erect; peduncles 13–40 cm long, 1–3 mm diam., longer than petioles; spathe membranaceous, red-violet, lanceolate to oblong-elliptic or ovate-elliptic, 1.3–2.5 cm long, 3–7 mm wide, abruptly acuminate at apex, rounded at base; spadix sessile, purplish-brown, 0.6–6 cm long, 2–4 mm diam. midway; flowers 4-lobed, 5–5.6 mm long, 3.8–4.3 mm wide, the sides jaggedly sigmoid; 2–3 flowers visible in the principal spiral, 3–4 flowers visible in alternate spiral; tepals matte to semiglossy, punctate and minutely papillate; pistils weakly emergent, the apex ± flat; stigma exserted, buttonlike, 0.8–0.9 mm wide; stamens emerging in scattered manner; anthers cream, ca. 0.7 mm long, inclined inward over pistil; thecae ovoid, slightly divaricate; pollen white. INFRUCTESCENCE pendent; peduncle to 60 cm long; spadix to 10 cm long, 1.5 cm diam.; berries bright red, ± globose, slightly longer than broad, 6–8 mm long; me-

socarp gelatinous, ± translucent, lacking raphide cells; seeds 2, cylindroid, rounded on both ends, ca. 4 mm long, 1.6–1.8 mm diam., with an oblique depression at one end and the other end greenish, sticky gelatinous appendages at both ends. Fig. 77.

The species is found from Guatemala and Belize to the Guianas, southern Brazil and Peru. It is also known in the West Indies from Trinidad and Hispañola. In Costa Rica and Panama, the species is known only from topical moist forest.

Anthurium gracile has a large root system that may sometimes become infested with black, stinging ants. It is distinguished by its thin, oblanceolate, epunctate leaves, persistent, intact cataphylls, the relatively few-flowered spadix, the whitish roots, and the bright red, globose berries.

Anthurium gracile has been confused with *A. friedrichsthalii,* which differs in having coriaceous, broadly linear leaves, conspicuously punctate on the lower surface, cataphylls that soon weather to persistent fibers, flowers more numerous on the spadix, and berries that are pale yellow-orange, broader than long, and truncate at the apex. *Anthurium gracile* is also confused with *A. bakeri* Hook. f., which has punctate leaves with a collective vein that is sunken and more conspicuous than the primary lateral veins.

Anthurium gracile is the only described species of section *Leptanthurium* and is either an extremely variable species or comprised of some additional undescribed sibling species in the Andes of South America (Croat, 1976).

BELIZE. BELIZE DISTRICT: Gracy Rock, *Gentle 1694* (MICH). STANN CREEK DISTRICT: Middlesex, *Gentle 2803* (MICH); Silk Grass Creek Reserve, *Gentle 2624A* (MICH); Stann Creek Railroad, *Gentle 2108A* (MICH); N of Victoria Peak, *Gentry 7954* (MO). TOLEDO DISTRICT: S of Columbia Forest Station, *Vanderveen 616, 618, 621* (MO); Monkey River, *Gentle 3804* (MICH).

COSTA RICA. ALAJUELA: vicinity of Las Chiles, *Holm & Iltis 653* (P). CARTAGO: vicinity of Turrialba, *Godfrey 66241* (MO); *Tonduz 8422* (BR). LIMÓN: vicinity of Siguerres, *Burger & Liesner 6921* (MO); N of Puerto Viejo, *Baker & Burger 91* (DUKE): Shirores, *Tonduz 9231* (BR).

GUATEMALA. IZABAL: vicinity Lechuga, *Steyermark 39615* (MO). PETÉN: vicinity El Ceibal, *Steyermark 46166* (MICH).

HONDURAS. ATLANTIDA: vicinity La Ceiba, *Yuncker et al. 8666* (MICH, NY, RS). YORO: village of Las Flores, *Yuncker et al. 8187* (MO).

NICARAGUA. BOACO: N of Río Las Cañas, *Stevens & Krukoff 5846* (MO). CHONTALES: E of Santo Tomás, *Neill 549, 7396* (MO). MATAGALPA: SW of Río Tuma bridge, *Stevens 6020* (MO). RÍO SAN JUAN: no other location, *Atwood 5169* (MO). ZELAYA: no other location, *Nichols 584* (MO); *Svenson 5100* (MO); NW of Alamikamba, *Stevens 8172* (MO); S of Cerro Bakan, *Vincelli 319A* (MO); N of El Empalme, *Stevens 8411, 8413* (MO); N of Limbaika, *Stevens 8254* (MO); road from Puerto Cabezas to Rosita, *Stevens 7925* (MO); vicinity Quebrada El Toro, along Río Iyas, *Vincelli 375* (MO); SW of Río Kukalaya, *Stevens 8505* (MO); E of Rosita, *Neill 4444* (MO); Road from Siuna to Matagalpa, *Stevens 7522* (MO); vicinity Siuna, *Neill 3807, 4151* (MO); W of Siuna, *Stevens 6899* (MO).

Anthurium hacumense Engl., Bot. Jahrb. Syst. 25: 363. 1898. TYPE: Costa Rica. Puntarenas: along banks of Río Hacum (Platanar) near Buenos-Aires, 250 m elev., *Tonduz 6536* (B, holotype; BR, CR, isotypes).

Rosulate, epiphyte; stem short; roots few, directed upward; cataphylls coriaceous, ca. 9 cm long, drying dark brown, weathering to coarse linear fibers. LEAVES ± erect; petioles sulcate, rounded to weakly angular abaxially, 2–12 cm long, 1–1.5 cm diam.; geniculum 2–2.5 cm long; blades narrowly to broadly oblanceolate, coriaceous, 25–81 cm long, 7.5–29 cm wide, acuminate at apex, attenuate at base; upper surface glossy, lower surface semiglossy, conspicuously punctate; midrib broad and flat at base above, soon becoming convexly raised, narrowing and sunken toward apex, acutely raised below; primary lateral veins 7–15 per side, departing midrib at 45° angle, sunken above, raised below, straight to collective vein; collective vein arising from base, sunken above, raised below, 1.5–2 cm from margin. INFLORESCENCE erect-spreading; peduncle 10–27 cm long, subterete; spathe subcoriaceous, yellow-green tinged with violet-purple, oblong-elliptic, 5.5–11 cm long, 2.2–3.5 cm wide, withering and early deciduous; stipe becoming elongate to 29 cm at anthesis; spadix purple-violet (B & K Red-purple 4/2.5), 10–20 cm long, 1–2.5 cm diam. at base, 7–12 mm diam. at apex; flowers sub-rhombic to 4-lobed, 2.4–3.6 mm long, 2–3.5 mm wide, the sides ± straight to jaggedly sigmoid; 9–20 flowers visible in the principal spiral, the alternate spiral irregular with 9–12 flowers visible; tepals glossy, with numerous tiny droplets; pistils flat to weakly emergent, pinkish to dark violet-purple, butterfly-shaped; the stigma oblong-elliptic, ca. 0.4 mm long, having minute droplets for several days before first stamens emerge; stamens emerging in a moderately prompt sequence from middle of spadix to both ends, the lateral stamens pre-

ceding alternates by several spirals, the stamens complete at apex before basal flowers complete, emitting a strong, sweet scent at anthesis; anthers dark violet-purple; exserted on fleshy, pale violet-purple filaments, soon retracting to level of tepals, held in a cluster covering pistils; thecae oblong, slightly divaricate; pollen white or cream turning lavender. INFRUCTESCENCE with spadix to 23 cm long; berries bright red (B & K Red 6/5), narrowly obovoid, acute to mammilliform at apex, ca. 1 cm long, 4–5 mm wide; seeds 2, white, weakly flattened, 2.5–2.7 mm long, 1.7–2 mm wide, 1–1.5 mm thick. Figs. 78 and 82.

The species is found from Costa Rica, Panama, and probably in Colombia in the Department of Chocó, ranging from sea level to 1,560 m and occurring principally in tropical wet forest, but also in premontane wet forest. In Costa Rica the species occurs in San José Province (El General Valley) and Puntarenas Province (Osa Peninsula and the adjacent valley of the Río Diguis). Although the species is restricted to the Pacific slope in Costa Rica, it is known in Panama only from the Atlantic slope and along the Continental Divide on the Pacific slope.

Anthurium hacumense is strikingly different from all other species and can easily be distinguished in flower or fruit by its exceptionally long stipe, the dark purplish-violet tepals, and bright red berries. Vegetatively the species can be recognized by the oblanceolate leaves with black punctations on the lower leaf surface and the conspicuous collective vein, (0.8)1–2.4 cm remote from the margin.

The species was placed by Engler in section *Pachyneurium* apparently owing to its large oblanceolate leaves and rosulate habit, but it should be placed instead in section *Porphyrochitonium* because of its glandular dotted lower surface and lack of involute leaf vernation.

Anthurium hacumense is perhaps most closely related to *A. curvilaminum* Croat (ined.), which also has short petioles, smaller but similarly coriaceous blades with a prominent collective vein relatively remote from the margin, and a spadix of precisely the same color, which has a pleasant aroma. The latter differs however in having a spadix that is essentially sessile whereas *A. hacumense* has a spadix which has a stipe equalling or often exceeding the length of the spadix.

COSTA RICA. CARTAGO: near Selva, *Taylor 11463* (NY). PUNTARENAS: Corcovado National Park, *Liesner 2849, 2851* (MO); N of Palmar Norte, *Croat 35194* (MO); Rincón de Osa, *Liesner 1698* (MO); *Utley 1190* (DUKE); Santo Domingo, *Engler 10094* (BR); Playa Blanca, *Valerio 323* (BR); vicinity San Vito de Java, *Croat 32903* (MO). SAN JOSÉ: between San Isidro del General & Dominical, *Croat 35340* (MO).

Anthurium halmoorei Croat, sp. nov. TYPE: Mexico. Nayarit: along Hwy. 28 between Tepic and Jalcocotán at Km 15.5, elev. ca. 1,000 m, *Croat 45337* (MO-2690192-193, holotype; CAS, K, MEXU, MICH, SEL, isotypes; Live at MO).

Planta epiphytica aut rupestris; caudex brevis, crassus, radicibus densis crassisque; petiolus 15–19 cm longus, 12–18 cm latus, lateribus complanatis, adaxile late sulcatus, abaxiale obtuse angulatus aut costatus; lamina oblanceolata aut oblanceolata-elliptica, subcoriacea, 52–108 cm longa, 15–43 cm lata, marginibus late undulatis, nervis primariis lateralibus ad marginem liberibus; inflorescentia effusa, foliis breviora; pedunculus 32–38 cm longus; spatha ovata aut ovata-elliptica, viridis, 13–16 cm longa; spadix viridis aut purpurata, 9–21 cm longa; baccae flavovirentes.

Rosulate, epiphyte or on rocks on very steep slopes; stems thick; internodes and leaf scars obscured by root mass; roots dense, descending, ca. 1 cm diam.; cataphylls subcoriaceous, 20–23 cm long, apiculate at apex, drying tan to brown, persisting intact at apex, dilacerating at base. LEAVES erect-spreading; petioles 15–19 cm long, 12–18 mm wide, flattened laterally, broadly sulcate adaxially, obtusely angular or 1-ribbed abaxially; geniculum 1–1.5 cm long; blades oblanceolate to oblanceolate-elliptic, subcoriaceous, short-acuminate at apex, attenuate at base, 52–108 cm long, 15–43 cm wide, broadest at middle or just above, the margins broadly undulate; the upper surface semiglossy, the lower surface matte and much paler; midrib broad and flat at base, convexly raised at middle, narrowed and flat at apex above, acutely raised below, the abaxial rib of the petiole extending onto midrib; primary lateral veins 12–14 per side, departing the midrib at a 40°–55° angle, prominently raised above, raised below; straight then curving toward apex near margin; interprimary veins less conspicuously raised above, visible and flat below; secondary veins prominulous above, flat below; collective vein arising from a primary lateral vein near the apex, 6–11 mm from margin, flat above, prominulous below. INFLORESCENCE spreading, shorter than leaves; peduncle 32–38 cm long, 9–10 mm diam., subterete, obscurely angled, 2–2.5 times longer than petioles; spathe subcoria-

ceous, green (B & K Yellow-green 6/10), sometimes tinged purple, ovate to broadly ovate, 13–16 cm long, 6.2–9.7 cm wide, broadest near base, acuminate at apex, acute at base, the margins undulate, inserted at a 70° angle on peduncle; spadix green, purple, or green heavily tinged purple (B & K Red-purple 2/5), 9–21 cm long, 11–27 mm diam. at base, 5–7 mm diam. at apex; flowers 4-lobed, 2.4–2.8 mm long, 2.7–3.2 mm wide, the sides sigmoid; 8–14 flowers visible in the principal spiral, 12–20 flowers visible in the alternate spiral; tepals matte, weakly punctate, minutely papillate, lateral tepals 1.5–1.8 mm long, the inner margin convex; pistil slightly raised, green tinged with purple in area of stigma; stigma linear, 0.4–0.6 mm long, a minute droplet appearing 4–5 days before first stamens emerge, dry with white exserted papillae when anthers open; stamens emerging ± rapidly from the base exserted on filament ca. 0.3 mm long, 0.8 mm wide, retracting to hold anthers held at edge of pistil, mounded with pollen; anthers orange; thecae ellipsoid, scarcely divaricate; pollen orange (B & K Yellow 7/2.5), drying white. INFRUCTESCENCE pendent; spathe usually persisting; berries irregularly obovoid, pale yellow green, broadly rounded to almost flat with a scurfy, brown square around style, 12–15 mm long, 7–9 mm diam.; mesocarp fleshy with numerous raphide cells; seeds 2, pale tan, subglobose, weakly flattened, 5–6.5 mm long, 3.5–4.1 mm wide, ca. 2.5 mm thick, with a sticky appendage at base and apex. Figs. 83 and 87.

Anthurium halmoorei is restricted to western Mexico in the states of Nayarit, Jalisco, Colima, and Michoacán in seasonally very dry forests from 450 to 1,450 m elevation. It occurs usually on rocks on very steep slopes in forested areas.

The species is in section *Pachyneurium* and is characterized by its generally oblanceolate or oblanceolate-elliptic blades with usually free-ending primary lateral veins, and by its petiole which is acute abaxially but especially by its ovate to ovate-elliptic spathe, green to purplish spadix and greenish-yellow mature berries.

The species is probably most closely related to *A. schlechtendalii* ssp. *jimenezii*, which differs in having the petiole subquadrangular, usually flat abaxially and in having a lanceolate spathe and red berries at maturity. That species occurs only in Guerrero and southern Oaxaca.

MEXICO. JALISCO: vicinity Autlán de Navarro, *McVaugh 10224* (MICH); *Wilbur 2289* (MICH); between El Tuito & Puerto Vallarta, *Delgado 359* (MICH); *Hernández 2608* (MEXU); *Anderson 6113* (ENCB, MICH); S of San Pedro, *Koeppen & Iltis 593* (BH); Talpa de Allende, *McVaugh 23408* (MICH). MICHOACÁN: vicinity Aguililla, *McVaugh 24741* (MICH); Coalcomán de Matamoros, *Rzedowski 16707* (ENCB, MICH). NAYARIT vicinity Jalcocotán, *Gentry & Gilly 10734* (MEXU, US); *McVaugh 12140* (MICH); *Moore & Bunting 8692* (BH); vicinity Jalisco, *Norris & Toranto, 12645* (CAS, MO); vicinity Mirador El Aguila, *McVaugh 15281* (MICH); NE of Santa María del Oro, *Feddema 703* (MICH); Tepic, *Bates et al. 1554* (BH); N of Tepic, *Dressler 339* (UC); NW of Tepic, *Lewis s.n.* (MICH); *Ferris 6816* (DS); W of Tepic, *Dressler 1024* (UC); between Tepic and Jalcocotán, *Croat 45337* (CAS, K, MEXU, MICH, MO, SEL).

Anthurium hoffmannii Schott, Oesterr. Bot. Z. 8: 181. 1858. TYPE: Costa Rica. San José: Chica Uruca, *Hoffmann 571* (B, destroyed; Photo of Schott Aroid Drawing #662, NYBG Neg. #N.S. 3897).

Anthurium torresianum Engl., Bot. Jahrb. Syst. 25: 428. 1898. LECTOTYPE: Costa Rica. San José: San Francisco de Guadalupe, 1,100 m, *Tonduz 7176* (US, hololectotype; F, M, NY, isolectotype; designated Croat & Baker, 1979).

Epiphyte or terrestrial; stems to 60 cm or longer; internodes 1–2 cm long; leaf scars obscured by cataphylls; roots few, green, 3–8 mm diam.; cataphylls coriaceous, 7–15 cm long, drying reddish brown, persisting intact. LEAVES with petiole erect-spreading, 20–90 cm long, 4–8 mm diam., terete or weakly sulcate; geniculum 2–3.5 cm long; blades ovate, moderately thick, 14–55 cm long, 9–38 cm wide, acuminate at apex, deeply lobed at base; anterior lobes 11–44 cm long, posterior lobes 4–12 cm long; sinus parabolic to spathulate; the upper surface semiglossy, the lower surface glossy; the midrib convexly raised above, acutely raised below; primary lateral veins 4–5 per side, weakly sunken above, raised below; basal veins 4–7 pairs, 3–4 coalesced 1–4 cm (rarely free to base); posterior rib naked, weakly turned upward; collective vein arising from first basal vein, sunken above, acutely raised below, 3–10 mm from margin. INFLORESCENCE erect to slightly arching; peduncle 16–50 cm long, 1–4 mm diam., terete; spathe, pale yellow-green, subcoriaceous, oblong-ovate to lanceolate, 6–13 cm long, 1.7–3 cm wide, inserted at 70° angle on peduncle; spadix stipitate 6–10 mm in front, 1–3 mm in back, pale green becoming white or cream colored, 4.5–8.5 cm long, ca. 8 mm diam. at middle, ca. 7 mm diam. at base and apex; flowers 4-lobed, 2.3–2.8 mm long, 2.6–3 mm wide, the sides straight to sigmoid, 5–8 flowers

FIGURES 83–86. 83. *Anthurium halmoorei* Croat, *Croat 45337* (Type).—84. *Anthurium hoffmannii* Schott, *Hammel 3471*.—85. *Anthurium huixtlense* Matuda, *Croat 40583*.—86. *Anthurium interruptum* Sodiro, *Selby 58-1975-32*.

FIGURES 87–90. 87. *Anthurium halmoorei* Croat, *Croat 45337* (Type).—88. *Anthurium hoffmannii* Schott, *Burger & Baker 10092*.—89. *Anthurium huixtlense* Matuda, *Croat 42673*.—90. *Anthurium kunthii* Poepp., *Croat 38121*.

visible in the principal spiral; 8–13 flowers visible per alternate spiral; tepals glossy, obscurely punctate, lateral tepals 1.4 mm wide, the inner margin ± straight; pistils weakly and acutely raised, white, minutely papillate; stigma linear, 0.3 mm long, a minute inconspicuous slit with minute droplets briefly apparent ca. 1 week before stamens emerge; stamens emerging rapidly, scattered throughout spadix, the lateral stamens first; anthers white, held in ± contiguous square at edge of pistil, 0.4–0.7 mm long; thecae ovoid, weakly divaricate; pollen white. INFRUCTESCENCE arching-pendent; spadix to 15 cm long, to 2 cm diam.; berries red, ovoid, ca. 8 mm long, ca. 5 mm wide; pericarp with elongate raphide cells; mesocarp clear, gelatinous; seeds 2, brown, ca. 4 mm long, ca. 2 mm wide. Figs. 84 and 88.

Anthurium hoffmannii is found in Costa Rica and Panama at elevations mostly between 700 and 1,700 m, principally in tropical wet, premontane rain and lower montane rain forest but also in premontane wet forest.

This species is in section *Calomystrium* and is closely related to (and perhaps not separate from) *A. huixtlense,* which ranges from Mexico (Chiapas) to northern Nicaragua, and to *A. monteverdense* from Costa Rica. It is also related to a number of unnamed taxa from Panama. All these species share a similar thick, ovate, prominently basally lobed blade, and thick, persistent cataphylls that dry reddish-brown and remain intact in age. Leaves generally have numerous short, linear, raphide cells on the upper surface which can be seen both before and after drying.

COSTA RICA. No other location, *Pittier 3867* (BR). ALAJUELA: no other location, *Austin Smith H991* (NY). CARTAGO, SE of Platanillo, *Croat 36725* (MO). PUNTARENAS: Boruca, *Pittier 4655* (BR); Buenos Aires, *Pittier 3869, 6538* (BR); Las Cruces Botanical Garden, *Croat 44396* (MO); Pan Am Highway, El General Valley, *Williams et al. 28810* (F, GH, WIS); W of Rincón de Osa, *Burger & Gentry 8923* (F, MO, US); E of San Isidro, *Webster et al. 12403* (US); S of San Vito, *Raven 21768* (F). SAN JOSÉ: no other location, *Luteyn 3282* (DUKE); *Pittier 455* (BR, UC, US); *Standley 42015, 42054* (US); Alajuelita, *Pittier 8839* (BR); vicinity Guadalupe, *Pittier 8485, 8764, 9858* (BR); *Tonduz 7176* (NY, US); vicinity San Isidro del General, *Burger & Baker 10092* (MO); *Burger & Visconti 10679* (MO); *Croat 35266* (MO); *Jiménez 3836* (F); *Molina et al. 17927* (CAS); *Skutch 3076* (GH, MO, NY).

Anthurium huixtlense Matuda, Revista Soc. Mex. Hist. Nat. 11: 91, Fig. 1. 1950. TYPE: Mexico. Chiapas: near Cerro Piedra de Huixtla, 20 km NE of Huixtla, 900 m elev. *Matuda 18615* (MEXU, holotype).

Anthurium bochilense Matuda, Bol. Soc. Bot. México 19: 21. 1956. TYPE. Mexico. Chiapas: Bochil, near San Cristóbal de Las Casas, *MacDougall 363* (MEXU, holotype).

Terrestrial or epiphytic; stems to 14 cm long, 3 cm diam.; leaf scars 2–3 cm wide, obscured by cataphylls at upper nodes; roots few, ca. 5 mm diam., descending; cataphylls coriaceous, 5–23 cm long, long-acuminate at apex (the acumen apiculate ca. 1–2 mm), drying dark tan (B & K Yellow 5/2.5), persisting intact. LEAVES erect-spreading; petioles 15–70 cm long, 6–9 mm diam., terete; geniculum 1–5 cm long; blades subcoriaceous, ovate to broadly ovate, 17–70 cm long, 10.5–36 cm wide, broadest just below point of petiole attachment, short-acuminate at apex, deeply lobed at base; anterior lobe 14–50 cm long, the margins rounded; posterior lobes 5–20 cm long, flat to downturned, sometimes overlapping; the sinus triangular to hippocrepiform, sometimes ± rhombic in larger leaves when flattened; the upper surface matte to semiglossy with sparse, obscure raphide cells, the lower surface glossy; the midrib sharply raised above, diminished and sunken at apex, convexly raised below; basal veins 5–6 pairs, the third to fifth coalesced 2–2.5 cm, raised; the posterior rib naked, turned up on the outer margin; primary lateral veins 3–5 per side, prominulous above and below, departing midrib at 30°–40° angle, straight or arching near collective vein; lesser veins less conspicuous; collective vein arising from one of the lowermost primary lateral veins or from the first basal vein, flat to weakly raised, 4–10 mm from margin. INFLORESCENCE erect-spreading, shorter than leaves; peduncle 21–39 cm long, 4–7 mm diam., terete; spathe coriaceous, pale whitish-green (B & K Yellow-green 9/10), oblong-lanceolate, 4.5–15 cm long, 2.7–4.5 cm wide, broadest at middle, abruptly long-acuminate at apex, obtuse to rounded at base; the stipe 12 mm long in front, 2.5 mm long in back, pale green; spadix reddish-violet to lavender (B & K Red 8/5, red-purple 5/2.5 to purple 6/5), rarely white, 4.2–20 cm long, 6–10 mm diam. at base, 5–6 mm diam. at apex; the flowers 4-lobed, 2.3–3.1 mm long, 2.5–3.5 mm wide, the sides jaggedly sigmoid; 5–8 flowers visible in the principal spiral, 5–9 flowers visible in the alternate spiral; tepals semiglossy, with white inconspicuous punctations, smooth to very minutely papillate,

lateral tepals 1.5–2.2 mm wide, the inner margin straight; pistil emergent, white, glossy; stigma 0.3–0.6 mm long, linear; stamens emerging moderately rapidly from the base, lateral stamens emerging to apex before alternates emerge at base, held in tight cluster obscuring pistil; anthers white to pale yellow, 0.6–0.7 mm long, 0.6–0.8 mm wide; thecae oblong, scarcely or not at all divaricate; pollen white. INFRUCTESCENCE spreading to pendent in large plants; spathe deciduous; spadix ca. 21 cm long, 2 cm wide; berries orange, globose; seeds green, up to 3 per berry. Figs. 85 and 89.

Anthurium huixtlense ranges from southern Mexico (Chiapas) to Nicaragua.

The species is a typical member of section *Calomystrium* and can be recognized by its thick, persistent cataphylls that turn reddish-brown and remain intact, and by its relatively long, usually reddish-violet to lavender spadix with early emergent pistils and orange berries. In *Flora of Guatemala* (Standley & Steyermark, 1958) this species was called *A. concinnatum,* an unrelated species from high elevations in Costa Rica and Panama.

The species is closely related to and is perhaps only subspecifically distinct from *A. hoffmannii,* which ranges from Costa Rica to Panama. *Anthurium hoffmannii* has a moderately thick green spathe and a white spadix. In addition, the tepals of *A. hoffmannii* are generally matte. In *A. huixtlense* the tepals are glossy and the pistil is rather prominently exserted (although usually soon hidden by the tight cluster of stamens) giving the spadix a coarse, almost "prickly" look. The spadix of *A. hoffmannii* has the pistils scarcely exserted at or near anthesis so that the spadix does not have a "prickly" look.

Spathe and spadix color are quite variable for *A. huixtlense.* Spathe color may be green to white and spadix color ranges from creamy white to lavender or reddish-violet. For some populations the color remains consistent but since considerable color variation may be found within a population the spadix color is not a useful taxonomic character in *A. huixtlense.*

The plants of *A. huixtlense* with lavender spadices are similar to those of *A. armeniense,* which has somewhat pinkish spadices and a white spathe. However, that species is distinguished by having the tepals matte rather than glossy and in having an early emergent pistil that is as long or longer than the stamens when they emerge.

Another close relative of both *A. hoffmannii* and *A. huixtlense* is *A. erythrostachyum* Croat (ined.) from Panama. The latter species differs from both of the former species by its caudate-acuminate spathe with the acumen up to 3 cm long. It differs also from *A. hoffmannii* in having the spadix colored somewhat lavender.

Anthurium huixtlense has been confused with *A. fraternum* Schott since the time of Engler. That species occurs in the Sierra Nevada de Santa Maria of northeastern Colombia. *Anthurium huixtlense* and *A. fraternum* share a similar leaf shape (as do most members of the section *Calomystrium*) and a similar spathe and spadix shape, but *A. fraternum* differs in having a dense array of discrete, punctiform, glandlike dots on the upper surface of the blade on drying and has a dense array of minute, reddish-brown blotches on the lower surface. *Anthurium fraternum* is not known from Central America.

BELIZE. CAYO DISTRICT: vicinity La Flor, *Croat 23784* (MO).

EL SALVADOR. SAN SALVADOR: La Palma, *Bernhardt s.n.* (MO).

GUATEMALA. ALTA VERAPAZ: vicinity Cobán, *Croat 41470, 41479* (MO); *Tuerckheim 3795* (GH); Finca Cubilhuitz, *Tuerckheim 8611* (GH); Río Cobán. *Johnson 723* (UC); N of church in Senahú. *Luteyn & Almeda 3524* (MO); W of Telemán, *Croat 41572* (MO). ESCUINTLA: Volcán de Fuego, *Standley 64529* (F). IZABAL: N of Highway CA9, *Harmon & Fuentes 1926* (MO). QUEZALTENANGO: vicinity Patzulín, *Standley 86887* (F). SAN MARCOS: Finca Armenia, *Dwyer 14459* (MO), SOLALÁ: Volcán Atitlán, *Steyermark 47997* (F, GH). SUCHITEPÉQUEZ: Santa Bárbara, *Lind 12* (WIS). ZACAPA: Volcán de Monos, *Steyermark 42387* (F).

HONDURAS. ATLANTIDA:vicinity La Ceiba, *Yuncker et al. 8741* (F, GH, MO); Lancetilla Valley, *Chickering 204* (MICH); *Croat 42673* (MO): *Standley 55668* (F); *Yuncker 4955* (MICH, MO); *5005* (MICH). COMAYAGUA: W of Siguatepeque, *Molina 25976* (F). CORTÉS: vicinity El Jaral, *Standley et al. 7060* (F); vicinity Peñas Blancas, *Hernandez & Hernandez 5302* (MO); Santa Cruz de Yojoa, *Edwards P-714* (GH). OCOTEPEQUE: vicinity Nueva Ocotopeque, *Molina & Molina 30950* (MO). SANTA BÁRBARA: NW side of Lake Yojoa, *Croat 42751* (MO); *Yuncker 4859* (MICH, MO).

MEXICO. CHIAPAS: Acacoyagua, *Matuda 17969* (MEXU); vicinity Berriozábal, *Miranda 6474* (MEXU). NE of Bochil, *Breedlove 10219* (CAS): Bochil. *MacDougall 363* (MEXU); Comaltitlán, *Matuda 17881* (MEXU); Huixtla, *Matuda 18599, 37686* (MEXU); N of Jitotol, *Thorne & Lathrop 46732* (RSA): Monserrate, *MacDougall 26026* (MEXU); vicinity Ocosingo. *Ton 3518* (DS, F, MICH); N of Ocozocoautla de Espinosa, *Croat 40583, 40633* (MO); vicinity Pueblo Nuevo Solistahuacán, *Croat 46428, 47773* (MO); vicinity San Fernando, *Miranda 6162* (MEXU): Munc. Tenejapa, *Breedlove 7560* (CAS); Tuxtla Gutiérrez.

MacDougall 375 (MEXU). VERACRUZ: Hidalgotitlán, *Valdivia 375, 686* (XAL); *Vazquez 51* (XAL).

NICARAGUA. No other location, *Williams et al. 24733* (F). NUEVA SEGOVIA: S of Jalapa, *Neill 1666* (MO).

Anthurium interruptum Sodiro, Anales Univ. Centr. Ecuador 15: 301. 1902. TYPE: Ecuador. Western slopes of the Cordillera de Angamarca, Nov. 1899. *Sodiro s.n.* (B, holotype).

Anthurium radicosum Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 210. 1947. TYPE: Guatemala. Alta Verapaz: along Río Icbolay, 300–350 m, 6 March 1942, *Steyermark 44776* (F, holotype).

Scandent epiphyte; stems elongate with 1 or more short internodes alternating with a long internode, 8–33 cm long, appearing to have several leaves at each node, often with a short, leafy, branch with several short internodes at these nodes; rooting profusely at each node; cataphylls 3–4.5 cm long, drying brown, dilacerating and ultimately deciduous. LEAVES spreading; petioles ± terete, 1.8–13 cm long; blades lanceolate to elliptic, oblong-elliptic or oblanceolate, subcoriaceous, 5–21 cm long, 2.2–9.5 cm wide, acuminate at apex, acute to rounded at base, 5–21 cm long; the midrib raised above, flat to prominulous below; primary lateral veins 9–12 per side, departing midrib at 45°–55° angle, ± obscure above, usually obscure below; collective vein arising from the base, prominulous above, flat below, 4–6 mm from the margin. INFLORESCENCE erect-spreading; peduncle 4.5–14 cm long, longer than petioles; spathe green, oblong-lanceolate, 3.7–5 cm long, 1–1.5 cm wide, acuminate at apex, acute at base; spadix green, becoming brownish-purple, 2.5–4 cm long; flowers 4-lobed, ca. 3 mm in both directions, the sides sigmoid; ca. 3 flowers visible in either spiral; pistils emergent, green, mammilliform; stamens held above tepals; anthers about as long as broad, less than 1 mm long; pollen pale yellow. INFRUCTESCENCE spreading-pendent; spadix to 12 cm long; berries red, broadly obovoid, ca. 7 mm long, flattened at apex with central depression. Figs. 86 and 95.

The species is known from Guatemala to Panama, Ecuador, and surely will be found also on the Pacific slope of Colombia. In Costa Rica and Panama it is known from premontane wet, tropical wet, premontane rain, and lower montane rain forest at elevations from 150 to 1,000 m. In Costa Rica the species is known on the Atlantic slope from northwestern Alajuela to southeastern Cartago Province. In Panama it is known from both the Atlantic and Pacific slopes.

Anthurium interruptum is in section *Xialophyllium* and can be recognized by its scandent stem with greatly, elongated internodes alternating with two or more successive abbreviated internodes giving the appearance of several leaves being clustered at a node. In addition, no other scandent, entire-leaved species is known to have bright red berries.

Anthurium interruptum most resembles *A. pittieri* and *A. carnosum.* Steyermark, in *Flora of Guatemala* (Standley & Steyermark, 1958), combined *A. radicosum* and *A. pittieri,* apparently due to their vegetative resemblance. However, *A. pittieri* can be differentiated by the long-decurrent spathe and shorter internodes. They also differ in altitudinal and geographical distribution. *Anthurium pittieri* is known only from Costa Rica and Panama while *A. interruptum* ranges from Guatemala to Ecuador. The former species also has a range of 50 to 2,100 m altitude but mostly above 1,000 m. In Ecuador the species may range to about 1,300 m. *Anthurium interruptum* is most common in the lowlands between 100 and 1,000 m. *Anthurium carnosum* differs from *A. interruptum* in its nearly uniform internode length, thicker leaves and altitudinal range of 1,500 to 2,600 m.

BELIZE. TOLEDO DISTRICT: Pueblo Viejo, *Schipp S-678* (MICH, MO, S).

COSTA RICA. ALAJUELA: vicinity Bijagua, along road to Upala, *Burger & Baker 9861* (MO); *Croat 36432* (MO). CARTAGO: road between Moravia & Quebrada Platanillo, *Croat 36631, 36655* (MO); SE of Platanillo, *Croat 36715* (MO); between Río Taus & Quebrada Azul, *Lent 2550* (MO); between Tuis and Bajo Pacuare, *Burger et al. 10029* (DUKE, MO, NY); Turrialba, along Río Reventazón, *Lent 693* (MO). HEREDIA: La Selva, Puerto Viejo de Sarapiquí, *Jiménez 101* (MO). LIMÓN: S of Siguirres, *Croat 43323* (MO).

NICARAGUA. ZELAYA: road to Colonia Agrícola Yolaina & Colonia La Esperanza, *Stevens 6311* (MO); *Vincelli 182* (MO); road from Siuna to Matagalpa, *Stevens 7521* (MO).

Anthurium kunthii Poepp. in Poepp. & Endl., Nov. Gen. et Spec. 3: 84. 1845. TYPE: Peru. Loreto: Maynas, *Poeppig s.n.* (W, destroyed; isotypes ?).

Epiphyte, scandent; stems usually to 1 m or longer, 1–1.5 cm diam., internodes 4–20 cm long; leaf scars 8–14 mm wide; roots numerous at each node, descending; cataphylls subcoriaceous, 2.5–8.5 cm long, drying yellow to tan (B & K Yellow-

red 9/10), persisting as linear fibers at each node. LEAVES spreading; petioles 20–60 cm long, 2–3 mm diam., terete, shallowly sulcate; geniculum 0.3–0.9 cm long, more deeply sulcate than petiole; blades ovate, 22–60 cm long, 20–40 cm wide, 5-, 7-, or 9-pedatisect, the leaflets moderately thin, elliptic to ovate-elliptic, 7–27 cm long, 3–8 mm wide, long-acuminate at apex, acute to attenuate at base; petiolules to 5.5 cm long, 1–2 mm diam., broadly and sharply sulcate; upper surface semiglossy, lower surface semiglossy to matte; midrib prominulous above, prominently raised below; primary lateral veins 5–18 per side, sunken above, raised below, departing midrib at 45°–55° angle, loop-connecting, weakly sunken above, raised below; collective vein arising from one of the lowermost primary lateral veins, 3–8 mm from margin. INFLORESCENCE spreading to arching, longer or shorter than the leaves; peduncle 20–55 cm long, terete; spathe green or sometimes slightly tinged purple, oblong-lanceolate, 5.5–15.5 cm long, 0.8–2.5 cm wide, acuminate at apex, acute to obtuse at base, inserted at 50°–70° angle on peduncle; stipe 5–9 mm long in front, 0.5–3.5 mm long in back; spadix pale green fading to tan at anthesis, 7–21 cm long, 5–10 mm diam. at base, 1–4 mm diam. at apex; the flowers rhombic to 4-lobed, 3.5–4 mm long, 2.5–3 mm wide, the sides straight to sigmoid; 5–9 flowers visible in the principal spiral, 5–7 flowers visible in the alternate spiral; tepals matte, minutely papillate, lateral tepals 1–1.5 mm long, the inner margin convex and upturned; pistils not emergent, pale green, matte, minutely papillate; stigma linear, ca. 0.5 mm long; stamens emerging slowly from base, the alternate pair emerging at base when the lateral stamens have emerged ca. one-third the length, held close around the pistil; anthers creamy white, 0.3–0.4 mm long, 0.6–0.9 mm wide; thecae ellipsoid, widely divaricate; pollen white. INFRUCTESCENCE pendent; spadix to 25 cm long; berries purple to violet-purple. Figs. 90 and 91.

Anthurium kunthii ranges from Costa Rica to Peru. In Costa Rica it is known only from tropical moist forest in Limón Province. In Panama it occurs in tropical moist and premontane wet forest on both slopes at elevations below 500 m.

Because of its palmately compound leaves, *A. kunthii* is confused only with *A. pentaphyllum* var. *bombacifolium*. *Anthurium kunthii* differs by having long, slender peduncles, nearly equalling the petioles in length, and by having a slender, elongate, usually greenish spadix. It also differs from *A. pentaphyllum* var. *bombacifolium* in having leaflets distinctly petiolulate and more or less equilateral at the base. *Anthurium pentaphyllum* var. *bombacifolium* usually has at least the outer leaflets inequilateral at the base, a short peduncle, and a pale violet-purple spadix. The species is a member of section *Dactylophyllium*.

COSTA RICA. LIMÓN: Talamanca, *Ocampo 1904* (MO). NICARAGUA. ZELAYA: Cerro Baká, Coperna; *Pipoly 4920* (MO).

Anthurium lancetillense Croat, sp. nov. TYPE: Honduras. Atlántida: Lancetilla Valley, ca. 10 mi SE of Tela; in forest preserve along Río Lancetilla, on trail to water reservoir, 10–150 m elev., *Croat 42672* (MO-2583478-79, holotype; EAP, K, MEXU, SEL, TEFH, US, isotypes; Live at MO).

Planta terrestris; caudex ad 15 cm longus; petiolus 17–82 cm longus, teres; lamina anguste ovata, 38–54 cm longa, 20–35 cm lata, basi cordata profunde; inflorescentia effusa-erecta, foliis breviora; pedunculus 3.5–36 cm longus; spatha viridis, interdum intra purpurea, lanceolata, 8.5–16 cm longa, 2–3.2 cm lata; spadix atropurpureus, 11–20.5 cm longus; pollen aurantiacum; baccae aurantiacae, ovoideae.

Terrestrial; stems to 15 cm long, 2.5–3 cm diam.; leaf scars conspicuous, 2.3–3 cm wide; roots tan, 6–8 mm diam., descending; cataphylls subcoriaceous, 9–13 cm long, acute at apex, minutely subapiculate, drying tan, dilacerating at base, remaining intact at apex, persisting around base of leaves. LEAVES with petioles erect, 17–82 cm long, 5–10 mm diam., terete; geniculum 1.5–3 cm long; blades narrowly ovate, moderately thick, gradually long-acuminate at apex, deeply lobed at base, 38–54 cm long, 20–35 cm wide, broadest midway between base and point of petiole attachment, margins weakly undulate; anterior lobe 24–37 cm long, the margins rounded to concave; posterior lobes 12–19 cm long; the sinus spathulate to hippocrepiform, acute to obtuse at apex; both surfaces semiglossy; the midrib convexly raised above, more acutely raised below; basal veins 6–7 pairs, first and second free, the remaining coalesced 3.5–4 cm; posterior vein naked, weakly curved, rolled conspicuously upward; primary lateral veins 3–4 per side, departing midrib at 45°–50° angle, raised at midrib, sunken near collective vein above, raised below; lesser veins less conspicuous, flat above

and below; collective vein arising from the first basal vein, sunken above, raised below, 2–10 mm from the margin. INFLORESCENCE erect-spreading, shorter than leaves; peduncle 3.5–36 cm long, 4–7 mm diam.; spathe subcoriaceous, green, sometimes heavily tinged with violet-purple on inner surface, lanceolate, 8.5–16 cm long, 2–3.2 cm wide, gradually long-acuminate at apex (the acumen inrolled ca. 3.5 cm) rounded at base, inserted at 45° angle on peduncle; spadix dark violet-purple (B & K Blue-purple 2/10), 11–20.5 cm long, 7–12 mm diam. at base, 3–5 mm diam. at apex; flowers rhombic to weakly 4-lobed, 3.3–5 mm long, 2.8–4.5 mm wide, the sides straight to weakly sigmoid; 5–7 flowers visible in the principal spiral, 4–12 visible in the alternate spiral; tepals matte, obscurely punctate, minutely papillate, lateral tepals 2.3–4 mm wide, the inner margin concave; pistils violet-purple around stigma, green below, weakly emergent; stigma ellipsoid, 1 mm long, opening ca. 2 weeks before first stamens emerge, large milky droplets apparent for several days, drying before first stamens emerge; stamens emerging in a relatively rapid sequence from the base, the lateral stamens emerging in basal one-quarter before alternates emerge, exserted on translucent filaments, 0.7 mm long, 0.5 mm wide; anthers pale orange, 0.6–0.7 mm long, ca. 0.8 mm wide, held in a contiguous cluster around pistil; thecae ovoid-ellipsoid, somewhat divaricate; pollen orange. INFRUCTESCENCE pendent; spathe persistent; spadix 10–23 cm long, developing berries in basal one-third to one-half; berries, orange, ovoid, 10–13 mm long, 8–11 mm diam., acute at apex; mesocarp juicy with numerous, minute raphide cells; seeds 1–2, pale green, ca. 6.8–8.0 mm long, 4.5–6.2 mm wide. Figs. 92 and 96.

Anthurium lancetillense is known only from Honduras in the Lancetilla Valley at elevation from 10 to 600 m. It occurs in wet forest.

The species is a member of section *Belolonchium* and is characterized by its narrowly ovate, moderately thick leaf blade, its green, subcoriaceous spathe that is sometimes tinged violet-purple on inner surface, its deep violet-purple spadix, orange pollen, and ovoid orange berries.

Anthurium lancetillense is most clearly related to *A. umbrosum*, which occurs only in Mexico in Oaxaca. It can be distinguished by its longer, more erect petioles and shorter more erect inflorescences. *Anthurium lancetillense* has larger, ovoid berries while *A. umbrosum* has smaller, globose berries with 4-radial ridges at apex. *Anthurium umbrosum* is also found at much higher elevations ranging from 1,200 to 1,800 m.

HONDURAS. ATLÁNTIDA: Lancetilla Valley, *Croat 42672* (EAP, K, MEXU, MO, SEL, TEFH, US); *Standley 53556* (F, US); *Webster et al. 12706* (DAV, US); vicinity of San Alejo, *Standley 7594* (F).

Anthurium lancifolium Schott, Oesterr. Bot. Z. 8: 180. 1858. TYPE: Costa Rica. Cartago: Volcán Turrialba, *Wendland 518* (GOET).

Anthurium allenii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 66. 1940. TYPE: Panama. Coclé: north rim of El Valle, elev. 800–1,000 m, *Allen 1854* (MO).

Anthurium firmum Engl., Bot. Jahrb. Syst. 25: 460. 1898. TYPE: Costa Rica. Puntarenas: Cañas Gordas, 1,100 m, *Pittier 11130* (B, holotype; BR, CR, isotypes).

Anthurium densinervium Engl., Bot. Jahrb. Syst. 25: 386. 1898. TYPE: Costa Rica. Along Río Hondo near Madre de Dios, elev. 200 m, *Pittier 10346* (CR, holotype; B, isotype).

Epiphyte or terrestrial, 30–90 cm tall; stems 1–1.5 cm diam.; the internodes very short; roots short, 3.5 mm diam.; leaf scars obscured by persisting cataphylls; cataphylls 4–7 cm long, drying reddish-brown weathering into coarse fibers. LEAVES spreading; petioles 15–45 cm long, 3–5 mm diam., obscurely and narrowly flattened adaxially sometimes with a faint medial rib; geniculum ca. 1.5 cm long, tinged purplish; blades subcoriaceous, lanceolate to ovate-lanceolate or oblong-elliptic, 20–30(50) cm long, 4–12 cm wide, long-acuminate at apex, cuneate at base; both surfaces semiglossy with black glandular punctations, more conspicuously so on lower surface; midrib narrowly and convexly raised above, becoming more acute at apex, prominently raised below; the primary lateral veins 15–25 per side, departing the midrib at 35° angle, sunken in valleys above, raised below; lesser veins obscure; collective vein arising from near the base, relatively straight, extending to the apex, 5–15 mm from the margin. INFLORESCENCE ± erect, shorter than leaves; peduncle 26–60 cm long; spathe green, oblong-lanceolate, 4.3–8.5 cm long, 0.8–1.9 cm wide, broadest at base, abruptly cuspidate at apex; spadix gray- or greenish-white, 4.5–9.5 cm long, 5–7 mm diam. at base, 4–5 mm diam. at apex; flowers rhombic to 4-lobed, 3–3.3 mm long, 3.3–3.6 mm wide, the sides straight to

broadly sigmoid; ca. 5 flowers visible in the principal spiral, ca. 8 flowers visible in the alternate spiral; tepals glossy, smooth, the lateral tepals ca. 2 mm long, the inner margin convex; the pistil emergent; stigma green, elliptic, ca. 3 mm long; stamens emerging 1 or 2 at a time, exserted on fleshy, flattened filaments; anthers white, held just above tepals, 0.5–0.8 mm in both directions; thecae not divaricate; pollen white. INFRUCTESCENCE pendent; spadix to 15 cm long; berries violet-purple, ovoid to globose, ca. 3–5 mm wide; mesocarp pulpy; seeds white, broadly ellipsoid, to 4 mm long, 3 mm wide, 2 mm thick, flattened. Fig. 93.

Anthurium lancifolium ranges from Costa Rica to Colombia (Antioquia and Chocó) at elevations of 100 to 1,600 m (especially 800 to 1,200 m) in regions of premontane wet, tropical wet, premontane rain, and lower montane rain forest life zones. It is the most common and widespread species in section *Porphyrochitonium* and is also one of the most variable. Blades vary in shape from linear-lanceolate to oblong-lanceolate to narrowly ovate with their dried coloration varying from green to olive-green to brown.

The species is recognized by its short stems with persistent, weathered cataphylls, frequently terrestrial habit, generally elongate, gradually acuminate, glandular-punctate blades that more or less equal the petiole in length, by the green, lanceolate spathe, and especially by the grayish-white, moderately short, weakly tapered spadix that has stamens persisting after anthesis, unlike most species in the section, that promptly retract their stamens. The species is known to have two varieties and more varieties or perhaps even distinct species are expected to be segregated from this variable, wide ranging species as living material of the group is studied in detail. The typical variety has dark violet-purple berries from the beginning of berry maturation, whereas the variety *albifructum* has berries that are white before maturity becoming faintly purple-violet at the base at maturity. Leaves of variety *albifructum* also differ from those of the typical variety found on Cerro Colorado where they occur together. Those of variety *albifructum* are narrowly ovate, rather than lanceolate, and dry yellowish-green on the lower surface. Most blades of the typical *lancifolium* dry rather dark.

Anthurium lancifolium is similar to *A. aureum* Engl. of South America, which has leaves drying golden green beneath.

A noteworthy collection (*D'Arcy 11259*) from Panama, in Colón Province at Río Iquanita (390 m elevation) may ultimately prove distinct. It has unusually small leaves, measuring only 21 × 4 cm but also has cataphylls that are not weathered to fibers as is the usual case in *A. lancifolium.*

COSTA RICA. ALAJUELA: near Cariblanco, *Burger & Antonio 11104* (MO). CARTAGO: between Moravia and Quebrada Platanillo, *Croat 36629, 36693* (MO); Volcán Turrialba, *Wendland 518* (GOET). HEREDIA: S of Cariblanco, *Croat 35793* (MO). LIMÓN: vicinity of Guapiles, *Standley 37512* (US). PUNTARENAS: Cañas Gordas, *Pittier & Tonduz 11130* (BR). SAN JOSÉ: Finca Navarro, *Maxon 669* (NY).

NICARAGUA. ZELAYA: vicinity Quebrada El Toro, along Río Iyas, *Vincelli 375A* (MO).

Anthurium lentii Croat & Baker, Brenesia 16 (Supl. 1): 56. 1979. TYPE: Panama. Chiriquí: vicinity of Cerro Colorado Mine Development, 28 miles above San Felix, 1,200–1,500 m, *Croat 33204* (MO-2381193, holotype; Live at MO).

Epiphyte or terrestrial, 56–120 cm tall; stems usually short, stout, 2–3 cm diam.; roots moderately dense, several at most nodes, ca. 6 mm thick, green or brownish, descending; cataphylls coriaceous, (5)8–19 cm long, turning brown, mucronate at apex, remaining intact, eventually dilacerating. LEAVES with petioles erect to erect-spreading, 10–70 cm long, (5)8–9 mm diam., broadly sulcate above sheath, more deeply sulcate near apex with acute margins, rounded abaxially, sometimes tinged purplish; geniculum 1–4.5 cm long, sulcate, usually purplish; blades ovate to narrowly ovate, coriaceous, semi-erect or spreading from petioles, rounded to retuse and apiculate at apex, truncate to subcordate or cordate at base, 15–50 cm long, 12.5–37 cm wide, broadest at point of petiole attachment, the margin pale green, often slightly turned under; the anterior lobe to 46 cm long with margins convex and often irregular where basal veins meet the margin; the posterior lobes to 14 cm long, directed conspicuously upward; the sinus very narrow to broad (when present), obtuse to acute at apex; the upper surface semiglossy, the lower surface matte or semiglossy, conspicuously brownish glandular-punctate; the midrib convexly raised above, diminished toward apex, convexly raised below and usually tinged purple; basal veins usually 3 or 4 pairs, sometimes with as many as 6 pairs on cordate blades, up to 4 of them coalesced 0.5–3 cm, sunken or raised in valleys near

the midrib on upper surface, sharply raised and often tinged purple on lower surface; posterior rib naked, curved; primary lateral veins 10–20 or more per side, departing midrib at 45° angle, slightly sunken or flat above, raised below; interprimary veins numerous, nearly as prominent as the primary lateral veins, usually flat above, slightly raised below; secondary veins numerous, ± straight and connecting pairs of basal veins, ± flat and nearly as prominent as the primary lateral veins above, slightly raised below; collective vein arising from uppermost basal vein, 2–5 cm from the margin midway on blade, raised at base above, sunken at apex, tinged purple below. INFLORESCENCE erect to spreading, usually much longer than leaves; peduncle 30–88 cm long, 5–10 mm diam., terete, frequently mottled with purple, 0.66 to 3 times as long as petioles; spathe coriaceous, green tinged with purple (B & K Yellow-green 6/7.5), narrowly ovate-oblong to oblong-lanceolate, 8–14 cm long, (2)2.8–3.9 cm wide, broadest just above point of attachment, abruptly acuminate at apex, obtuse to acute at base, the margins often tinged purple, inserted at 45°–80° angle on peduncle; stipe 5–25 mm long in front, 2–6 mm long in back, ca. 8 mm wide, green, often mottled with purple; spadix violet-purple (B & K Red-purple 3/10), 12–25 cm long, 8–13 mm diam. at base, 5–8 mm diam. at apex, sometimes weakly arched in basal fourth; flowers rhombic, 2.8–4.5 mm long, 2.3–3.5 mm wide, the sides straight to weakly sigmoid; 7–13(15) flowers visible in the principal spiral, 5–8(10) flowers visible in the alternate spiral; tepals glossy, green-punctate, with small droplets at anthesis, lateral tepals 2–2.3 mm wide, the inner margins ± straight, not overlapping; pistils green, exposed at base as soon as the spathe opens; stigma ca. 1 mm long, green, usually square or hour-glass-shaped, brushlike with a small droplet appearing briefly, 1 or 2 days before the first stamens emerge, the papillae exserted above the tepals; stamens emerging moderately rapidly from the base, held in a close circle at edge of pistil; anthers white, held over pistil, opening as soon as they emerge, ca. 0.5 mm long, 1.5 mm wide; thecae ellipsoid, not divaricate; pollen white. INFRUCTESCENCE spreading; spathe persisting, the spadix 29–38 cm long, 1.5–2.5 cm diam.; berries oblong-linear, square in cross-section, tapered to ± square at apex, ca. 10 mm long, pale green, white at maturity, exserted from tepals 2–5 mm before maturity, often not maturing in apical one-half to one-fifth of the spadix. Seeds not seen. Figs. 94 and 97.

The species ranges from Costa Rica to Colombia (mountains of northwest Chocó adjacent to Panama) at elevations of 350 to 1,800 m. It occurs only along the central cordillera. In Costa Rica the species is known only from premontane rain and lower montane rain forest in the region around Tapantí but it possibly extends throughout the Talamanca mountain range. In Panama, the species has been collected in premontane wet, tropical wet, and lower montane wet forest from Cerro Colorado in Chiriquí Province to the Cerro Jefe region in Panamá Province, then appears again only near the Colombian border in Darién.

Anthurium lentii is in section *Digitinervium* and is perhaps most closely related to *A. ovatifolium* Engl., a species from Ecuador and Peru, which differs in having red berries. *Anthurium lentii* can be recognized by its thick, distinctively bicolorous, heavily punctate, truncate to cordate leaf blades with several, heavy, prominently ascending basal veins. Other distinctive features include the prominently exserted pistils and the white, oblong, more or less tetragonal mature berries.

COSTA RICA. CARTAGO: road between Moravia & Quebrada Platanillo, *Croat 36591* (MO); beside Río Taus, SW of Taus, *Lent 2989* (F); N of Tapantí, *Lent 2219* (F, US); near Tapantí, N by ENE of Tapantí, *Baker et al. 217* (CR, F, K, MO, US); Río Grande de Orosi, W of Tapantí, *Lent 907, 908* (CR, F).

Anthurium leuconeurum Lem., Ill. Hort. 9, Pl. 314. 1862. TYPE: The description is based on a plant from southern Mexico collected by Ghiesbrecht and cultivated in Ghent, Belgium, by Ambr. Vershchaffelt; the illustration in Ill. Hort. (9: 5.314. 1862) serves as the type.

Terrestrial; stems and internodes very short; cataphylls moderately coriaceous, acute at apex, persistent. LEAVES erect-spreading; petioles 30–70 cm long, 4–7 mm diam., terete or weakly sulcate adaxially, the blades held parallel to petiole; geniculum 1.5–3.5 cm long; blades narrowly ovate to ovate; abruptly acuminate at apex, deeply lobed at base, (12)20–38 cm long, (8)12–29 cm wide, broadest at point of petiole attachment; the anterior lobe (8)14–28 cm long; posterior lobes (2.5)6–13 cm long, directed toward base; the sinus obovate to hippocrepiform, rounded at apex; the upper surface velvety, dark green, the lower surface much paler; midrib and basal veins flat to weakly sunken above, much paler than sur-

face; the area on either side of the veins paler than rest of blade; basal veins 5–6(7) pairs, at least the third and fourth coalesced 1–4.5 cm, arcuate-ascending, the second and sometimes the third joining the margin well above the middle of the blade; the posterior ribs straight to gradually curved, naked (at least on the larger blades); primary lateral veins 3–4 per side, departing the midrib at an acute angle, then gradually curved toward the margin, loop-connecting with collective vein; collective vein arising from the first basal vein or sometimes one of the lowermost primary lateral veins, 0.7–1.4 cm from margin. INFLORESCENCE erect, at least as long as leaves; peduncle 40–68 cm long, 4–6 mm diam., terete; spathe narrowly ovate to ovate-lanceolate, green, 4.5–10 cm long, 1–2.5(3.5) cm wide, broadest just above base, narrowly acuminate at apex, weakly cordate and clasping at base, inserted at ca. 20° angle on peduncle; spadix sessile or nearly so, green, (4)6–13 cm long, 6–8 mm diam. at base, 4–5 mm diam. at apex; the flowers rhombic, 3.8–4 mm long, 3–3.5 mm wide, the sides straight parallel to spirals, smoothly sigmoid perpendicular to spirals; 6–7 flowers visible in the principal spiral, 4–5 flowers visible in the alternate spiral; tepals sparsely punctate, lateral tepals 2.1 mm wide, the margin broadly rounded, thin and turned up against pistil; pistils elevated but not emergent until after anthesis of stamens; the stigma 0.5 mm long, elliptic, slitlike; stamens emerging in a prompt sequence from the base, the stamens in the basal one-third complete before the alternates emerge in the apical one-third; anthers held above tepals and over pistil but not obscuring stigma, 0.9 mm long, 0.8 mm wide, evenly spaced; thecae oblong-elliptic, scarcely divaricate. INFRUCTESCENSE pendent; berries broadly obovoid, rounded at apex, bright orange, 9–10 mm long, 8–10 mm diam.; pericarp moderately thick, with dense raphide cells; seeds 2, narrowly obovoid to obovoid, brown(?), slightly flattened, 6–7 mm long, 5–6.5 mm wide, 3.6–4 mm thick. Fig. 98.

Anthurium leuconeurum was collected in southern Mexico in about 1860 and apparently has not been recollected in the wild. All known herbarium collections are from living collections, presumably derived from the original living collection in Belgium. If the species still exists in the wild it is surely a narrow endemic similar to *A. clarinervium*. I have strong suspicions that *A. leuconeurum* represents a plant of hybrid origin, probably offspring of *A. berriozabalense* and *A. clarinervium*. This cross has been made by Banta [see Aroideana 6(1): 26–27. 1983] and the resulting hybrid looks much like the type drawing of *A. leuconeurum*.

The species is a member of section *Cardiolonchium* and is characterized by having a velvety leaf blade with usually paler major veins similar to *A. clarinervium*, to which it is apparently related. It is distinguished from the latter species by its generally larger and more narrowly ovate leaves that have the basal veins coalesced into a naked posterior rib, 1–4.5 cm long. *Anthurium clarinervium* generally has the basal veins free or if they are coalesced the posterior rib is never naked.

Engler (1905) cites *Ghiesbreght (1877)* (note difference in spelling). It is not certain whether this is his collecting number or not but it implies that he saw an actual specimen. If so, it is unlikely that the specimen still exists.

Anthurium leuconeurum was the subject of much hybridization after its introduction into Europe in the early 1860s. Perhaps the most well known of these hybrids is *A. macrolobum* Hort. (*A. dentatum* André is a synonym), which is a cross between *A. leuconeurum* and *A. pedatoradiatum*.

Although the species was originally described by Lemaire as acaulescent and epiphytic, it was no doubt a terrestrial plant with a definite (although short) stem.

Since all known collections have been made from living collections in cultivation, no specimens are complete with the stem. In addition I have seen no bonafide living collection of the species. Because of these shortcomings the description is less complete than most.

MEXICO. Cultivated at California Botanical Garden *54.1349* (UC); cultivated at Fairchild Tropical Garden. *Frantz 3288* (FTG).

Anthurium lezamae Matuda, Bol. Soc. Bot. México 19: 19. 1956. TYPE: Mexico. Chiapas; Mun. Bochil, Bochil (cultivated in San Cristóbal de Las Casas), *MacDougall 362* (originally collected by W. Lezama) (MEXU, holotype).

Terrestrial; the stems short, 1.5 cm diam., internodes very close; cataphylls thin, 5–7 cm long.

drying reddish-brown, soon weathering at least at base into thin, mostly longitudinally oriented fibers. LEAVES with petioles 17–41 cm long, 2–4 mm diam., terete; geniculum 1–1.5 cm long; blades ovate to ovate-triangular, gradually acuminate at apex, deeply lobed at base, 13–28 cm long, 9–18.5 cm wide, broadest at the middle or at the base, the margin slightly hyaline (on drying), weakly revolute; anterior lobe 12.5–20.5 cm long, the margin almost straight to broadly rounded, (sometimes somewhat bulged at base of lobe), the margins sometimes somewhat variable with one margin slightly convex, the other slightly concave; the posterior lobes directed downward or slightly outward, 6–11.5 cm long, 3.5–6.5 cm wide; the sinus usually obovate, rarely parabolic, rounded or obtuse at apex; the upper surface with the epidermis drying with a characteristically raised, alveolate reticulation (papillate when fresh), the lower surface drying more or less smooth; the midrib raised on both surfaces; basal veins 4–5(6) pairs raised on both surfaces, the third and fourth (fifth) coalesced 4.5–6 cm, all but the uppermost arcuate-ascending, joining the margin, the second basal vein joining the margin well above the sinus and sometimes well above the middle of the blade; the primary lateral veins 2–3 per side, usually scarcely apparent, departing the midrib at 70°–80° angle, sometimes curving laterally at almost a 90° angle to the midrib, prominulous above and below, scarcely or not at all more prominent than the interprimary veins or tertiary veins; the tertiary veins weakly raised above and below; the collective vein arising from the uppermost basal vein, 5–13 mm from the margin, weakly raised on both surfaces. INFLORESCENCE usually held erect, well above the leaves; peduncles 37–78 cm long, 3–4 mm diam., longer than the petioles; spathe weakly coriaceous, green, lanceolate to oblong-lanceolate, 3.7–6.5 cm long, 7–14 mm wide, broadest just above the base or at the middle, acuminate at apex, weakly cordate and somewhat clasping at base, inserted at a 45° angle on the peduncle; stipe 2–4 mm long in front, 1–3 mm long in back; spadix greenish, 4–6.5 cm long, 5–6 mm diam. at base, 3–4 mm diam. at apex, held at 180° angle from peduncle; flowers rhombic, 3–4 mm long, (dry) 2.5–2.8 mm wide, (dry) the sides straight, parallel to spiral, gradually sigmoid perpendicular to the spiral; 4–6 flowers visible in the principal spiral, 3–4 flowers visible in the alternate spiral; tepals weakly glossy, minutely and densely punctate, lateral tepals 1.8–2 mm wide, the inner margin very broadly rounded, the alternate pair with inner margins straight to concave; pistil greenish, not emergent; stigma ca. 1 mm long, linear; stamens emerging promptly, from the base, the lateral stamens preceding the third and fourth stamens by only a few spirals, held just above the tepals in a close circle around the stigma; anthers 0.5 mm long, 0.7 mm wide; thecae semicircular, flat, not at all divaricate. INFRUCTESCENCE not seen. Figs. 99 and 100.

Anthurium lezamae is endemic to Mexico, in northern Chiapas at 900 to 1,500 m elevation. It is known from the municipios of Bochil, El Bosque, and Ocosingo. The plants grow on usually steep, rocky slopes in pine-oak forest in seasonally dry areas. A specimen from adjacent Oaxaca (*Schultes & Reko 867*, ECON) is possibly also this species but it has a broader spathe and lacks the typically alveolate epidermal pattern on the upper blade surface.

The species is a member of section *Cardiolonchium* and is recognized by its narrowly ovate-cordate leaf blades with the poorly developed primary lateral veins scarcely more prominent than the interprimary veins and the tertiary veins. Also characteristic is the unusual reticulation created by the epidermal cells on drying.

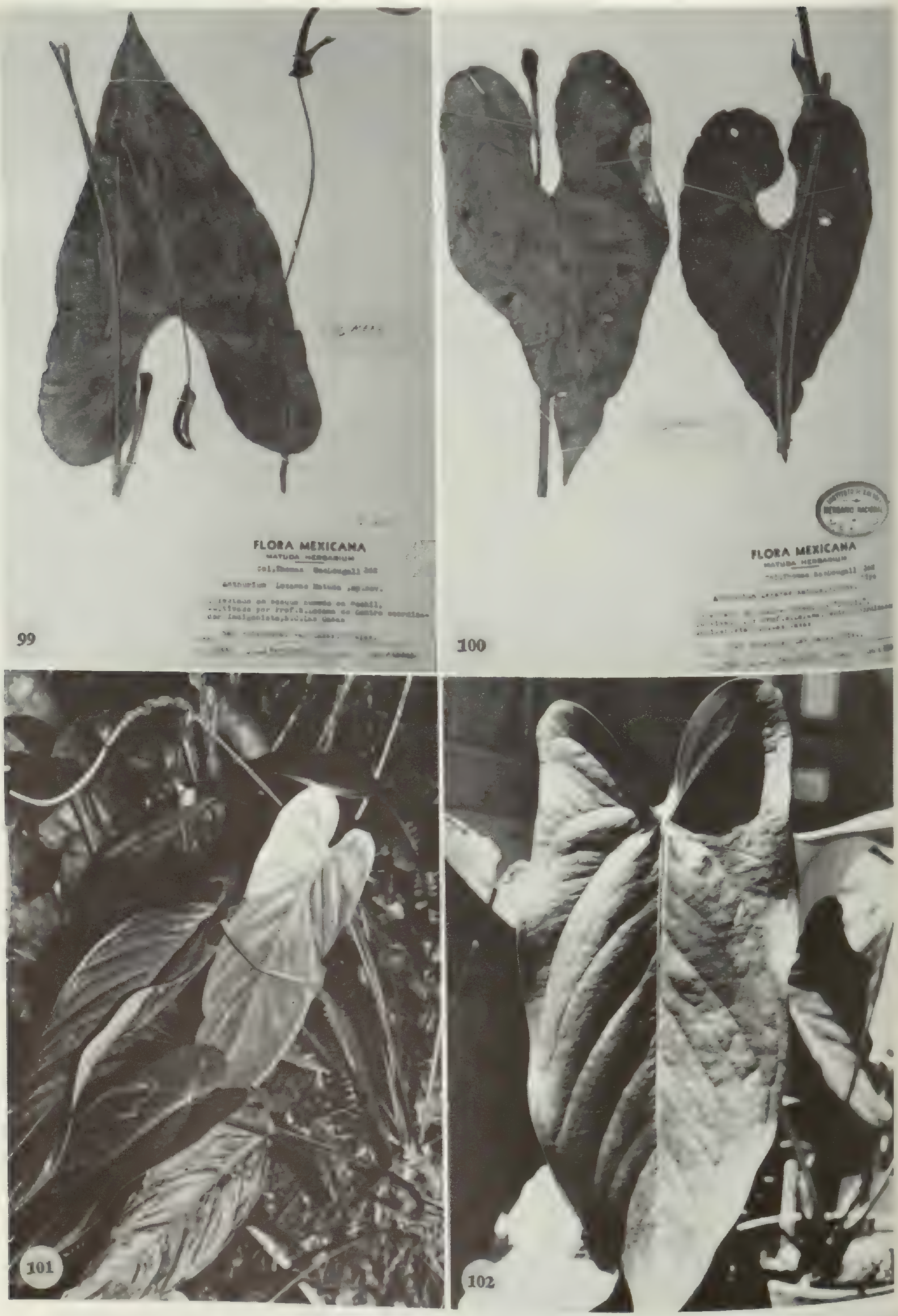
The species is perhaps most closely related to (and possibly inseparable from) *A. leuconeurum*, which differs in having the midrib and basal veins (and the area immediately adjacent to them) much paler than the rest of the blade surface. In addition, the blade surface of *A. leuconeurum* dries obviously papillate with the individual papillae distinguishable, whereas *A. lezamae* dries with the epidermal cells drying minutely alveolate (honey-combed). Unfortunately, *A. lezamae* has not been studied alive so I do not understand the significance of these differences.

MacDougall 302 and two unnumbered MacDougall collections from an area believed to be southwestern Oaxaca (between La Gloria and Río Grande and between Buena Vista and La Gloria) differ from *A. lezamae* only slightly in leaf shape but lack the alveolate epidermal pattern on the leaves typical of that species. It is possible that these represent a distinct species but too little is known about them to be certain.

MEXICO. CHIAPAS: vicinity of Jitotol, *Breedlove & Dressler 29832* (DS); *Breedlove & Smith 32558* (DS);

FIGURES 91–94. 91. *Anthurium kunthii* Poepp., *Croat 38121*.—92. *Anthurium lancetillense* Croat, *Croat 42672* (Type).—93. *Anthurium lancifolium* Schott, *Croat 27095*.—94. *Anthurium lentii* Croat & Baker, *Croat 37220*.

FIGURES 95–98. 95. *Anthurium interruptum* Sodiro, *Selby 58-1975-32*.—96. *Anthurium lancetillense* Croat, *Croat 42672*.—97. *Anthurium lentii* Croat & Baker, *Las Cruces Bot. Gard*.—98. *Anthurium leuconeurum* Lem., (Cultivated at McLain's, Ayr, Australia).



FIGURES 99–102. 99–100. *Anthurium lezamae* Matuda, *MacDougall 362* (Type).—101. *Anthurium longipeltatum* Matuda, *Croat 48326*.—102. *Anthurium longipeltatum* Matuda, *Croat 39755*.

vicinity Ocosingo, *Breedlove 27925* (DS); San Cristóbal de Las Casas, *MacDougall 362* (MEXU). OAXACA: between La Gloria & Río Grande, *MacDougall s.n. 302* (MEXU).

Anthurium longipeltatum Matuda, Anales Inst. Biol. Univ. Nac. México 37: 75, Fig. 1. 1967. TYPE: Mexico. Oaxaca: between Vista Hermosa and Puerto Eligio, Comaltepec Ixtlán de Juárez, elev. 1,200 m in humid forest, October 5, 1963, *MacDougall 563* (MEXU, holotype).

Epiphyte or terrestrial; stems green, ca. 18 cm long, 2.5–3 cm diam.; roots few, dark greenish-brown, descending; leaf scars 2–3 cm wide; cataphylls coriaceous, 6.5–15 cm long, long-acuminate at apex, drying dark brown, splitting at base, subpersistent. LEAVES with petioles erect to spreading, 29–56 cm long, 5–7 mm diam., terete; geniculum 1–4.5 cm long; blades oblanceolate to oblong-ovate, moderately thick, long-acuminate at apex, lobed at base, 33–56 cm long, 14–28 cm wide, broadest just below middle; anterior lobe 34–40.5 cm long, the margins convex; posterior lobes 4.5–10 cm long; the sinus parabolic to triangular, sometimes the lobes overlapping, acute at apex; upper surface semiglossy to glossy, lower surface semiglossy, obscurely to conspicuously punctate; the midrib prominulous, convex above, more prominently raised below; basal veins 3–5 pairs, usually free, sunken or prominulous in valleys above, raised below; primary lateral veins 8–12 per side, departing midrib at 35°–50° angle, sunken above, raised below, arcuate-ascending to collective vein; lesser veins flat to weakly sunken above, flat below; collective vein arising from the first basal vein, sunken above, raised below, 5–10 mm from margin. INFLORESCENCE erect-spreading, longer than leaves; peduncle 30–80 cm long, 3–8 mm diam., terete; spathe subcoriaceous, green sometimes faintly tinged purplish (B & K Yellow-green 8/10), oblong-lanceolate, 9–14.5 cm long, 1.5–2.2 cm wide, narrowly acuminate at apex, obtuse at base, inserted on peduncle at 30°–50° angle; spadix olive-green (B & K Yellow-green 6/5) to dark purple (B & K Blue-purple 2/10), 9–35 cm long, 7–9 mm diam. at base, 2–4 mm diam. at apex; flowers rhombic to 4-lobed, 2.5–4 mm long, 2.3–3 mm wide, the sides ± straight parallel to spiral, gradually sigmoid perpendicular to spiral; 6–7 flowers visible in the principal spiral, 7–9 flowers visible in the alternate spiral; tepals glossy, minutely papillate, sometimes with droplets as stamens emerge, lateral tepals 0.8–1 mm wide, the inner margin broadly rounded; pistils weakly emergent, green tinged with red-violet; stigma oblong-linear, 0.5–0.6 mm long, purplish with droplets apparent a few days before stamens emerge; stamens emerging from the base, the lateral stamens preceding alternates by 1–2 spirals, exserted briefly on pinkish flattened filaments, which retract, holding stamens at edge of tepals against pistil; anthers pale yellow, held ± contiguous, 0.3–0.4 mm long, 0.5–0.6 mm wide; thecae ellipsoid; pollen yellow to white, fading to cream. INFRUCTESCENCE pendent, spathe withered; berries subglobose to obovoid, rounded at apex, red to red-orange (B & K Red 6/7.5), 8–8.5 mm long, 5.5–6.5 mm wide; mesocarp fleshy, ± transparent with raphide cells; seeds 1–2, ovoid, cream or greenish-white, 4 mm long, 2.5 mm wide, 2 mm thick with sticky appendages at both ends. Figs. 101, 102, and 104.

The species occurs in northern Oaxaca, Sierra de Juárez, Veracruz near Orizaba, and is expected in nearby Puebla in Mexico in tropical wet forest from 600 to 1,500 m elevation.

The species is a member of section *Belolonchium* and is distinguished by its moderately thick, deeply lobed, oblong-ovate blades, which are dark green above and paler below, by its long slender spadix, by having basal veins frequently free with little or no posterior rib, and red to red-orange, subglobose berries.

The collections of *A. longipeltatum* from northern Oaxaca are somewhat obscurely punctate whereas those collected near Valle Nacional are more conspicuously punctate. The spadix color varies from olive-green to violet-purple.

Anthurium longipeltatum may be confused with *A. verapazense*, a species ranging from Belize to Honduras, but that species has a consistently violet-purple spadix and usually has a well developed posterior rib.

Matuda considered *A. longipeltatum* to be similar to *A. titanium* (*A. xanthosomifolium*) but it is in no way similar or related except that the two species have posterior lobes. *Anthurium titanium* differs principally in lacking punctate dots on the lower blade surface.

The etymology of the name is curious. Although Matuda named the plant "longipeltata" there is no part peltate. Perhaps this is a typographical error from the intended "longipetiolatum."

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FIGURE 103. *Anthurium louisii* Croat & Baker. *Field Museum Drawing 82395.*

FIGURES 104–107. 104. *Anthurium longipeltatum* Matuda, *Croat 48326*.—105. *Anthurium lucens* Standl. ex Yuncker, *Croat 41541*.—106. *Anthurium michelii* Guillaumin, *Croat 33142*.—107. *Anthurium microspadix* Schott, *Croat 40906*.

MEXICO. OAXACA: Comaltepec, *MacDougall 563* (MEXU); road from Teotitlán del Camino to Santa María Chilchotla, *Croat 48326, 48366* (MO); vicinity Valle Nacional, *Croat 39755, 39795, 43906, 43914, 47973, 48064* (MO); *King 2143* (MICH); *Moore & Bunting 8917* (BH); summit of Cerro de Cuhuatepete, vicinity Tehuacán, *Vera Santos 3340* (MICH).

Anthurium louisii Croat & Baker, Brenesia 16 (Supl. 1): 59. 1979. TYPE: Costa Rica. Cartago: about 2.5 km north by east northeast of Tapantí, 9°45'N, 83°47'W, 1,500–1,600 m elevation; forest remnants on steep slopes, *Baker, Utley & Utley 220* (F-1758200, holotype; MO-2385464, isotype.

Epiphyte or terrestrial, to 30 cm tall; stems erect, to 1 cm diam.; internodes 1–4 cm long; leaf scars obscured by cataphyll fibers; cataphylls 4–7 cm long, gradually acuminate at apex, drying brown, quickly weathering into coarse persistent fibers. LEAVES dispersed along stem at each node; petioles (15)20–30 cm long, ca. 3 mm diam., terete, narrowly sulcate; geniculum ca. 1.5 cm long; blades ovate to broadly ovate, subcoriaceous, gradually to abruptly long-acuminate at apex, obtuse or truncate to rounded at base, 14–17 cm long, 8–13.5 cm wide, broadest slightly below the middle; both surfaces conspicuously glandular-punctate; midrib raised above, diminished toward apex, prominently raised below; primary lateral veins 15–20 per side, departing midrib at 45° angle, ± straight, loop-connected by the collective vein, raised above and below; lesser veins inconspicuous; collective vein arising from the base, 4–12 mm from the margin. INFLORESCENCE, erect-spreading; peduncle (15)25–38(45) cm long, considerably longer than the leaves; spathe somewhat thin, green becoming reddish, lanceolate-linear, 4–6.5 cm long, ca. 1 cm wide, broadest at base, gradually acuminate at apex, slightly clasping at base, inserted at ca. 20° angle on peduncle; stipe very short or absent; spadix green to yellow-green, usually coiled at maturity, (4)6–18 cm long, 3–4 mm diam. at base, 2–3 mm diam. at apex (dry); flowers rhombic, 2–3.5 mm long, 2–2.5 mm wide; the sides ± straight; 2–3 flowers visible in either spiral; lateral tepals 1.6–2.1 mm wide, the inner margin broadly rounded; pistil green; stigma ca. 0.5 mm long, ellipsoid; stamens probably weakly exserted above the tepals, well spaced; filaments ca. 0.2 mm long; anthers ovate, 0.4–0.5 mm long, 0.5–0.6 mm wide; thecae ellipsoid, slightly divaricate. INFRUCTESCENCE with the spathe at least sometimes deciduous; spadix 8–15 cm long, 3–4 mm diam., usually coiled in age; berries ovoid to subglobose, green becoming orange-red, ca. 6 mm long and 5 mm wide, maturing simultaneously throughout the spadix, drying with a buttonlike beak. Fig. 103.

Anthurium louisii is known only from Costa Rica in premontane or lower montane rain forest, apparently restricted to middle elevations on the Atlantic slopes of the Cordillera Central and the Cordillera de Talamanca, 1,300 to 1,800 m.

The species is in section *Porphyrochitonium* and can be recognized by its broadly ovate leaves with glandular punctations on both surfaces and by its usually coiled spadix (in fruit). The type collection was found on a steep bank and formed the dominant ground cover.

Anthurium louisii is related to *A. angusturense* Engl. from Colombia. The latter species differs chiefly by its lanceolate leaf blades. *Anthurium louisii* also resembles *A. circinatum* Croat from Panama in Chiriquí Province.

COSTA RICA. CARTAGO: NNE of Tapantí, *Baker, Utley & Utley 220* (CR, DUKE, EAP, F, MO, NY, SEL, US); S of Tapantí, *Lent 1384* (F); on road between Tapantí and Tausito-Selva area, *Utley & Utley 2995* (F); Tapantí Hydroelectric Project, along trail to meteorological station, *Utley & Utley 4532* (DUKE); road from Tapantí to Taus and Tausito, NE of Río Grande de Orosi at Tapantí, *Utley & Utley 5035* (DUKE); near Copey, Cordillera de Talamanca, *Williams & Allen 16506* (EAP, F); region beyond Muñeco, 3 km from village church, SW of Orosi, *Utley & Utley 1839* (F). SAN JOSÉ: La Palma, Coronado, *Werklé s.n.* (CR).

Anthurium lucens Standl. ex Yuncker, Field Mus. Nat. Hist., Bot. Ser. 17: 317, Pl. 5. 1938. TYPE: Honduras. Comayagua: near El Achiote, hills above the plains of Siguatepeque, elev. 1,350 m, *Yuncker, Dawson & Vouse 5844* (F, holotype; GH, MICH, MO, US, isotypes).

Anthurium seamayense Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 4, Pl. 5. 1940. TYPE: Guatemala. Alta Verapaz: Seraxcaj, Finca Seamay, virgin forest, elev. 960 m, *C. L. Wilson* (F 968018, holotype).

Anthurium yunckeri Standl. ex Yuncker, Field Mus. Nat. Hist., Bot. Ser. 17: 317, Pl. 6. 1938. TYPE: Honduras. Comayagua: near El Achiote; hills above the plains of Siguatepeque, elev. 1,350 m, *Yuncker, Dawson & Vouse 5935* (F 857684, holotype).

Anthurium mapastepecense Matuda, Anales Inst. Biol. Univ. Nac. México 27: 339. 1957. TYPE: Mexico. Chiapas: Mapastepec, Finca Prusia, elev. 1,000

m, *MacDougall 337* (MEXU 109434, holotype; CAS, isotype).

Epiphyte or terrestrial; stems to 20 cm long, ca. 4.5 cm diam.; internodes and leaf scars obscured by roots and cataphylls; roots dark brown, medium thick, descending; cataphylls subcoriaceous, 6.5–7.5 cm long, heavily tinged red-violet, the apex acuminate with subapical apiculum 2–3 mm long, drying brown (B & K Yellow 4/7.5), weathering to persistent reticulate fibers, the apex remaining ± intact. LEAVES with petioles erect to spreading, (12)26–72 cm long, 0.6–1 cm diam., subterete; geniculum 2.5–3.5 cm long, sometimes faintly tinged red-violet; blades narrowly ovate to oblong-ovate or ovate-triangular, moderately thick, gradually acuminate at apex, deeply lobed at base, 30–46 cm long, 18–24 cm wide, broadest at the base or just below point of petiole attachment; the anterior lobe 22–32 cm long, the margins usually convex, sometimes ± straight; posterior lobes 10–16 cm long, the sinus spathulate to hippocrepiform, obtuse to rounded, or sometimes acute at apex; both surfaces semiglossy, the lower surface punctate; the midrib acutely to convexly raised above, convexly raised below; basal veins 5–6 pairs, the first and second free, the remaining coalesced 2–2.5 cm; posterior rib naked one half to one third its length, usually with inner margin turned up; primary lateral veins 2–7 per side, departing midrib at 55°–60° angle, straight or weakly curving to collective vein, sunken above, raised below; lesser veins scarcely visible above, visible and ± flat below; collective vein arising from the first basal vein, in larger blades from fourth or sometimes fifth basal veins, sunken above, raised below, 6–15 mm from the margin. INFLORESCENCE usually held erect, arching or pendent in larger plants, shorter than or equalling petioles; peduncle 33–75 cm long, 5–8 mm diam., terete, sometimes tinged red-violet; spathe moderately thin, green heavily tinged with red-violet, lanceolate, 4–8.5 cm long, 1.4–1.7 cm wide, narrowly acuminate at apex, rounded at base, inserted at 45° angle on peduncle; spadix deep violet-purple, 10.5–13 cm long, 9–10 mm diam. at base, 3–3.5 mm diam. at apex; flowers rhombic to weakly 4-lobed, 3–3.2 mm long, 2.6–3 mm wide, the sides straight to gradually or jaggedly sigmoid and somewhat obscure; 6–7 flowers visible in the principal spiral, 8–9 flowers visible in the alternate spiral; tepals matte to weakly glossy, weakly punctate, minutely papillate, with scattered droplets, lateral tepals 1.5–1.6 mm wide, the inner margin broadly rounded; pistils weakly raised, green, sometimes purplish; stigma linear, ca. 0.6 mm long, opening as stamens emerge; stamens emerging from the base in a moderately rapid sequence, the laterals first, soon followed by alternates, the leading stamens several spirals ahead of third or fourth stamens; anthers bright yellow, held at the edge of tepals, ca. 0.6 mm long, ca. 0.3 mm wide; thecae ovate, widely divaricate; pollen pale yellow. INFRUCTESCENCE pendent; the spathe usually deciduous; berries bright red, obovoid to oblong-ellipsoid, usually developing only in basal one quarter to one third, round to truncate at apex, 8–18 mm long, 6.5–18.5 mm diam.; mesocarp juicy, clear, with raphide cells; seeds 1–2, greenish white, oblong-elliptic, slightly flattened, 4–5 mm long, 2.5–4 mm wide, 1.8–2.1 mm thick, obliquely concave at apex. Figs. 105 and 108.

Anthurium lucens ranges from Mexico (State of Chiapas) to Honduras usually from 350 to 1,500 m (rarely to as low as 150 m in Guatemala to as high as 2,000 m in Chiapas). In Mexico the species occurs only in "bosque pino-encino" and "selva alta perennifolia" in northern Chiapas. In Guatemala it has been collected only in the departments of Huehuetenango, Alta Verapaz and Izabal.

Leaf shape is extremely variable in *A. lucens* but all populations share in common coriaceous, punctate leaf blades, an inflorescence shorter than or equal in length to the petiole, a relatively short violet-purple spadix with a spathe usually more than half as long as the spadix at anthesis, and red, obovoid, 1–2-seeded berries. Generally the anterior lobe of the blade is convex along the margins, although rarely the margins are concave and are similar to *A. chiapasense* except that they dry greenish to greenish brown and not blackened as is the case with *A. chiapasense*.

Honduran collections of *A. lucens* are somewhat unusual in that they are geographically isolated, the species not usually collected in southern Guatemala.

Other collections worthy of mention are those of *MacDougall 337* (type of *A. mapastepecense*) and *Matuda 19647*. While both of these collections are unusual in being south of the range of most *A. lucens* and in having anterior lobes somewhat broader than normal, they are believed to be within the range of variability for *A. lucens* considering that the species is so widespread and variable.

FIGURES 108–111. 108. *Anthurium lucens* Standl. ex Yuncker, *Croat 41541*.—109. *Anthurium machetioides* Matuda, *Ramirez 144* (Type).—110. *Anthurium microspadix* Schott, *Croat 40906*.—111. *Anthurium montanum* Hemsl., *Croat 47161*.

Anthurium lucens is in section *Belolonchium* and is easily confused with *A. verapazense,* but that species is distinguished by having the inflorescence 1.5 to 3 times longer than the petioles, and by having the spathe generally less than half as long as the spadix at anthesis.

Berry and seed size are quite variable in *A. lucens.* For example while *Croat 41541* has berries ca. 7 mm long and seeds ca. 4 mm long, *Breedlove 9709* and *4308* have berries 11 to 14 mm long and seeds 7 to 8.5 mm long respectively. *Breedlove 9709* is particularly noteworthy in having a very large fruiting spadix, drying ca. 3 cm in diameter. Nevertheless the berries and seeds appear to be qualitatively similar and are all believed to represent the same species.

GUATEMALA. ALTA VERAPAZ: vicinity Telemán, *Croat 41541* (MO); Cerro Chinajá, *Steyermark 45570* (F, MO); *45624* (F, LL); *45649* (F); vicinity Finca Cubilhuitz, *Steyermark 44740* (F); Finca Sipacate, *Cook & Griggs 434* (US); Seraxcaj, Finca Seamay, *Wilson 211* (F); vicinity of Panzós. *Croat 41612, 41697* (MO). HUEHUETENANGO: near Barillas, *Steyermark 49736* (F, US). IZABAL: El Estor, *Harmon & Dwyer 4340* (MEXU, MO); NW of Lake Izabal, *Jones & Facey 3389* (NY); along Río Bonito, *Steyermark 41723* (F, US).

HONDURAS. COMAYAGUA: between San Antonio & El Cedral, *Molina 22588* (F, NY); vicinity Siguatepeque, *Williams & Molina 18083* (F); above the plains of Siguatepeque, *Yuncker et al. 5844* (F, GH, MICH, MO, U, US); *5935* (F).

MEXICO. CHIAPAS: SE of Comitán, *Carlson 1913, 2334* (MEXU); *2294* (MICH); Munc. Tenejapa, *Breedlove 10968* (DS); *Ton 1574* (CAS, DS, MEXU); E of La Trinitaria, *Breedlove 9709* (CAS, DS, ENCB, F); *14971* (DS, LL, MEXU); *Breedlove & Raven 11308* (DS, CAS); *13027* (DS); *Breedlove & Thorne 21226, 27581A* (DS); *Breedlove & Smith 32104* (DS); Montebello National Park, *Breedlove & Dressler 29535* (DS); *Breedlove 38754* (DS); Munc. Ocosingo, *Dressler 1452* (GH, MICH, NY, US); NW of Ocozocoautla de Espinosa, *Breedlove 27500* (DS); Cascada Siltepec, *Matuda 19647* (MEXU); between Palenque & Bonampak, *Croat 40222* (MO); E of San Quintín, *Breedlove 33385* (CAS, DS).

Anthurium machetioides Matuda, Anales Inst. Biol. Univ. Nac. México 22: 379, Fig. 7. 1952. TYPE: Mexico. Oaxaca? (see discussion): Chinantla, 1,200 m, *Ramirez 144* (MEXU, holotype).

Stems short, internodes short; cataphylls thin, to 6.5 cm long, drying brown, weathering to linear fibers, probably deciduous. LEAVES with petioles 6–7 cm long, 4–5 mm diam., broadly sulcate adaxially, rounded abaxially; geniculum 4–5 mm long; blades oblanceolate, narrowly acuminate at apex, narrowly cuneate at base, 45–48 cm long, 6–8 cm wide, broadest above middle, matte on both surfaces (dry); the midrib prominently and narrowly raised above and below (dry); primary lateral veins 10–15 per side, departing midrib at 20°–30° angle, curving down and joining collective vein; reticulate venation prominulous in dry specimens; collective vein arising from one of the primary lateral veins near the base, 3–4 mm from margin. INFLORESCENCE equalling or longer than leaves; peduncle 40–48 cm long, to 5 mm diam., terete; spathe narrowly lanceolate, inserted at 45° angle on peduncle; spadix green, 20–24 cm long, 1.3 cm diam. at base, 6 mm diam. at apex; the flowers rhombic, 2–2.4 mm long, 2.4–2.6 mm wide; 13–14 flowers visible in the principal spiral, 9–10 flowers visible in the alternate spiral; pistils not emergent; stigma elliptic, slitlike, 0.5 mm long; stamens held level with tepals; anthers ovate. INFRUCTESCENCE not seen. Fig. 109.

Anthurium machetioides is endemic to central Mexico on the Atlantic slope. The type was from the region of Chinantla in northeastern Oaxaca (a region comprising part of 4 districts south of Valle Nacional), at 1,200 m and a second collection was made relatively near at 200 m in the District of Tuxtepec (probably San José Tuxtepec between Valle Nacional and Tuxtepec).

The species is characterized by its oblong-linear leaves with a collective vein from near the base and primary lateral veins that are scarcely more prominent than the tertiary veins, and by the very elongate gradually tapered spadix.

In describing the species Matuda indicated its relationship as section *Leptanthurium*; however, despite the fact that it has a collective vein from the base, its affinities are most likely with *Anthurium schlechtendalii* in section *Pachyneurium,* which often has a collective vein from near the base in juvenile leaves. It differs from *A. schlechtendalii* in its proportionally narrower leaves, the collective vein and by its proportionately much longer spadix.

MEXICO. OAXACA: near Chinantla, *Ramirez 144* (MEXU); Tuxtepec, *Martinez-Calderon 844* (MICH).

Anthurium michelii Guillaumin, Bull. Mus. Hist. Nat. (Paris) 31: 263. 1925. TYPE: Panama. Bocas del Toro: hills beyond Fish Creek Lagoon, *Wedel 2276* (P, holotype).

Anthurium amethystinum Croat & Baker, Brenesia 16 (Supl. 1): 20. 1979. TYPE: Costa Rica. Cartago: along road between Moravia (east of Tuis, SE of Turrialba) and Quebrada Platanillo, 3–5 km from

Finca Racine in Moravia; elev. 1,200–1,300 m; disturbed primary forest, *Croat 36601* (MO 2395446, holotype; CR, F, K, NY, SEL, US, isotypes; Live plant at MO).

Epiphytic or terrestrial; stem usually very short, 6–25 cm long, 1.5–3 cm diam.; roots dense, 1.5–5 mm thick, descending; cataphylls subcoriaceous, 8–23 cm long, cordate-acuminate at apex, drying brown (B & K Red 9/2.5), persisting, weathering into fibers. LEAVES held nearly erect; petioles 9–25 (40) cm long, 5–9 mm diam., flattened laterally, sulcate with sharp margins, acute to rounded abaxially; geniculum 1–1.6 cm long; blades elliptic to oblong-elliptic or oblong, gradually acuminate at apex (the acumen downturned), acute to obtuse at base, 8–54 cm long, 5.5–22 cm wide, broadest at the middle or slightly below the middle, the margin ± flat, continuous with margins of the petiole; both surfaces matte to semiglossy; midrib convexly raised and diminished toward apex above, acutely raised below; basal veins consisting only of the lowest pair of primary lateral veins; primary lateral veins 6–15 per side, sunken above, prominulous below; interprimary veins weakly sunken above, prominulous below; collective vein moderately straight, prominent, continuous, arising from the second pair of primary lateral veins, sunken above, prominently raised below, 5–9 mm from the margin. INFLORESCENCE pendent or arching-pendent, usually shorter than the leaves; peduncle 30–58 cm long, 3–5 mm diam., much longer than petioles, prominently 4- or 5-ribbed especially near the base, irregularly striate toward apex with one prominent sharp rib arising from beneath the spathe; spathe coriaceous, medium green (B & K Yellow-green 7/10), oblong-lanceolate to oblong, 3–15 cm long, 1–2.5 cm wide, broadest in lower third, inserted at 45° angle on peduncle; stipe 0.8–3.5 cm long; spadix yellow-green (B & K Yellow-green 6/7.5), (4.5) 8.5–20 cm long, 6–10 mm diam. at base, 4–6 mm diam. at apex; flowers rhombic, 3–4.2 mm long, 2.8–4.3 mm wide, the sides straight to jaggedly sigmoid; (4)7–11 flowers visible in the principal spiral, 5–7 flowers visible in the alternate spiral; tepals green, semiglossy, sometimes with scattered nectar droplets; lateral tepals 2–2.7 mm wide, the inner margin ± straight, somewhat turned up against pistil; pistils exserted 0.5 mm, pointed before maturity, the exserted portion broadly ovoid; stigma linear, 0.4–0.6 mm long, exserted, brushlike, with conspicuous droplets for about 10 days, becoming dry and brown, about 1 week before first stamens emerge, dry and exserted when stamens emerge; the lateral stamens emerging rapidly from the base, open in basal three-quarters before the first alternates begin to emerge at the base, sometimes emerging in a more scattered fashion, held in a close circle around pistil; anthers white, 0.5–0.6(0.8) mm long, 0.4–1 mm wide; thecae elliptical, opening flat, moderately divaricate; pollen white. INFRUCTESCENCE becoming pendent; the spathe light green; the spadix 5–20 cm long, 2–3 cm diam.; berries obovoid to ovoid or pyramidal, pointed at apex, glossy, dark purple to violet-purple, 7–12 mm long when dry, paler violet-purple in lower third; mesocarp gelatinous; seeds 2, flattened, ca. 5 mm long, 4 mm wide, 3 mm thick. Fig. 106.

The species is known from Costa Rica and Panama on both slopes at altitudes from 400 to 1,400 m, mostly in premontane wet and tropical wet forest.

Anthurium michelii is distinctive for its creamy green or whitish underleaf surface and bright purple berries. Also characteristic are the oblong-elliptic leaves, broadly and sharply sulcate petiole, and the frequently conspicuously stipitate spadix.

The species is a somewhat atypical member of section *Pachyneurium*, and appears to be unrelated to any other species in the section.

The type specimen of *A. michelii*, not studied until recently, is aberrant and unusually small for the species and, despite the fact that it bears little resemblance to the type of *A. amethystinum*, the two are now known to represent the same species.

COSTA RICA. ALAJUELA: La Balsa de San Ramón, *Utley & Utley 1850* (F); Hacienda la Marina, Río San Rafael, canton de Aguas Zarcas, *Williams et al. 2914* (F); E of Río San Rafael & S of the hot springs. W of La Marina, *Burger & Stolze 5002* (F); La Palma de San Ramón, *Brenes 5599* (CR, F); Methodist Rural Center Quebrada Marín, E of Ciudad Quesada, *Burger & Stolze 4994* (CR, F, MO, NY); San Luis de Zarcero, *Austin Smith NY1258* (F, NY); road from Cariblanco to Lake Hule, W of Hwy. 9, *Baker, Utley & Utley 223*[illegible] (F); NW of Cariblanco, *Luteyn 3348* (DUKE); NNE of Bijagua along the new road to Upala, *Burger & Baker 9862* (F, MO); *9862A* (F). CARTAGO: Moravia de Chirripó, *Ocampo 1166* (CR); along Camino Raiz de Hule, SE of Platanillo, *Croat 36743* (MO); along road between Moravia and Quebrada Platanillo, *Croat 3660*[illegible] (CR, F, K, MO, NY, SEL, US). HEREDIA: vicinity of Colonia Virgen del Socorro, E of Cariblanco on the finca of Sr. Carolo Molina, *Utley & Utley 2827* (F). SAN JOSÉ: La Hondura, *Standley 36313* (US); Las Lajas,

Leon 1148 (CR); along road from San Isidro del General to Dominical, *Burger & Baker 10106* (F); *Croat 35259* (MO); 1 mile beyond divide between San Isidro del General and Dominical, *Croat 35323* (MO).

Anthurium microspadix Schott, Oesterr. Bot. Z. 8: 180. 1858. Type: Costa Rica, near Naranjo, *Oersted s.n.* (Type not found; Photo of Schott Aroid Drawing #322, NYBG Neg. #N.S. 3812).

Anthurium porrectum Schott, Oesterr. Bot. Z. 8: 180. 1858. Type: Costa Rica, near Desengaño, *Wendland 841* (GOET).
Anthurium tapinostachyum Schott, Oesterr. Bot. Z. 8: 180. 1858. Type: Costa Rica, near Candelaria, Alto de La Cruz, *Hoffmann s.n.* (Photo of Schott Aroid Drawing #331, NYBG Neg. #N.S. 3818).
Anthurium colombianum Engl., Bot. Jahrb. Syst. 25: 379. 1898. Type: Colombia. Putomayo: valley of Sibundoy near Santiago, E of Pasto, elev. 2,000–2,500 m.
Anthurium tuerckheimii Engl., Bot. Jahrb. Syst. 25: 380. 1898. Type: Guatemala. Alta Verapaz: Pansamalá, 1,200 m, *Tuerckheim 864* (B, holotype; K, US, isotypes).
Anthurium gracilescens Sodiro, Anales Univ. Centr. Ecuador 15: 393. 1902. Type: Ecuador. Pichincha: Nanegal, *Sodiro s.n.* (B).
Anthurium lepturum Sodiro, Anales Univ. Centr. Ecuador 15: 458. 1902. Type: Ecuador. Pichincha: western slopes of Volcán Pichincha, *Sodiro s.n.* (B).
Anthurium nanegalense Sodiro, Anales Univ. Centr. Ecuador 15: 460. 1902. Type: Ecuador. Pichincha: Gualea, *Sodiro s.n.* (B).
Anthurium silvaticum Sodiro, Anales Univ. Centr. Ecuador 22: 25. 1907. Type: Ecuador. Tungurahua, *Sodiro s.n.*
Anthurium barbanum K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 9: 270. 1925. Type: Costa Rica. Near Barba, *A. C. Brade 2510* (B).
Anthurium gracilens Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 68. 1940. Type: Panama. Chiriquí: Río Chiriquí Viejo Valley, 1,300–2,000 m, *White 160* (F, holotype; MO, isotypes).

Scandent epiphyte or semierect, terrestrial herb; stems elongate, frequently to 1 m or more long, 4–7 mm diam., sparsely long-rooted at the nodes; the internodes (0.6)1–8(11) cm long; cataphylls thin, 4.5–7.5(11) cm long, acute and apiculate at apex, promptly weathering, soon deciduous, sometimes with a few pale fibers persisting. LEAVES persisting at the upper 6–10 or so nodes; petioles erect-spreading, subterete, narrowly and shallowly sulcate, 5–16(24) cm long, 2–2.3 mm diam.; geniculum 5–10 mm long; blades usually ± oblong, sometimes lanceolate, narrowly oblong-elliptic or oblong-ovate, abruptly or gradually acuminate at apex, usually truncate to rounded at base, sometimes acute or subcordate, 9–25 cm long, 2.5–11 cm wide, moderately thin; the upper surface semiglossy; midrib raised in a valley above, diminished and sunken toward the apex, prominently raised below; primary lateral veins 4–11 per side, departing midrib at ca. 45° angle, sunken above, raised below, straight or slightly curving to collective vein; interprimary veins usually present; tertiary veins usually prominent on lower surface; basal veins 1–3 pairs, usually free at base, all but the uppermost soon joining the margin; collective vein arising from the first basal vein, 2–5 mm from the margin. INFLORESCENCE erect, shorter than the leaves; peduncle terete, 5–15 cm long; spathe lanceolate-elliptic, olive-green or pale green, sometimes tinged purplish, 3–4(5) cm long, to 1.7 cm wide, abruptly acuminate at apex, weakly cordate at base, inserted at 45°–50° angle on peduncle; stipe usually 2–5 mm long, sometimes absent, or to 10 mm long; spadix pale yellow to yellow-green or green, sometimes tinged with purple, 1.5–4 cm long at anthesis, usually 4–5 mm diam. near base, 3–3.5 mm diam. near the apex; flowers square to weakly 4-lobed, 2.5–3 mm wide in both directions, the sides straight to jaggedly sigmoid; 4–6 flowers visible in the principal spiral, 6–7 flowers visible in the alternate spiral; tepals semiglossy, minutely papillate, large nectar droplets scattered over the surface when anthers are emerging, lateral tepals 1.5–2 mm wide, the inner margin broadly convex; pistil weakly emergent, medium green, slightly darker than tepals, semiglossy; stigma colorless, raised, brushlike, ca. 0.5 mm long, with stigmatic droplets 1–3 days before anthers emerge; stamens emerging slowly from the base, the laterals preceding the third and fourth stamens by only a few spirals; anthers cream, inclined over pistil, ca. 0.5 mm long, ca. 0.8 mm wide; thecae ovate-elliptic, slightly divaricate; pollen creamy white. INFRUCTESCENCE with spadix to 8 cm long, to 2.5 cm diam.; berries yellowish-green, subglobose, ca. 5 mm diam. Figs. 107 and 110.

The species ranges from Mexico to Ecuador at elevations from 800 to 2,300 m in premontane rain, lower montane wet, and lower montane rain forest. It is one of the most variable species of *Anthurium* in North America. In Panama it is most easily confused with *A. pallens* (see that species for a discussion of the differences).

In South America it is apparently closely related to *A. amoenum* Kunth in Peru and Bolivia,

A. tenuicaule Engl., and *A. brachypodum* Sodiro from Ecuador.

Sodiro described several species based on the presence or absence of a stipe, the comparative lengths of the peduncle and petioles, and the shape and relative size of the spathe in relation to the length of the spadix. These characters have been observed to be too variable even within a single population to warrant their use in the separation of species.

Anthurium microspadix has been placed in section *Xialophyllium.*

Mention should be made of an error in the translation of Lehmann's handwritten label by Engler. The type locality should read "Sibundoy" rather than "Dibundog."

Belize. Camp 32, Guatemala Survey, *Schipp S-679* (NY).

Costa Rica. No other location, *Bogner s.n.* (MO); *Pittier 66, 3863* (BR); *Tonduz 1888* (BR). alajuela, guanacaste, puntarenas: at juncture of provinces, *Burger et al. 10835* (MO) . alajuela: no other location, *Brenes 13611a* (NY); Peñas Blancas, *Kennedy & Guindon 3707* (MO); N of Los Ángeles de San Ramón, *Almeda & Nakai 3848* (MO); N of San Ramón, *Utley 4590* (DUKE, MO); Volcán Barba, *Tissine 1600* (WIS); S of Zapote, *Utley 4655* (DUKE); vicinity Zarcero, *Croat 43564* (MO); *Smith 115, 404, 485* (MO); *638, 826, 1124* (NY). cartago: trail to Meterological Station, *Utley 4536* (DUKE); between Moravia & Quebrada Platanillo, *Croat 36617, 36677* (MO); SW of Muñeco, *Luteyn 3873* (DUKE); S of Muñeco, *Utley & Utley 771* (MO); vicinity Palo Verde, *Luteyn 3329* (DUKE); *Luteyn & Wilbur 4381* (DUKE); vicinity Platanillo, *Croat 36819* (MO); between Quebrada Honda and the Río Sombrero, *Luteyn 3237* (DUKE); near forest above Río Taus, *Taylor & Taylor 11459* (NY); vicinity Tapantí, *Baker 212* (MO); *Burger & Liesner 6722* (MO); *Burger & Burger 7547* (MO); *Lent 1035* (NY); *Utley & Utley 5190* (DUKE); Tapantí Hydroelectric Reserve, *Croat 36175, 36217* (MO). guanacaste: near Monte Verde, *Weston 5063* (MO, NY); between Santa Elena & Monteverde, *Croat 47119* (MO). heredia: vicinity Bajo La Hondura, *Croat 44503* (MO); S of Cariblanco, *Croat 35847* (MO); Río Las Vueltas, *Taylor 17705* (NY); Tarrazu, *Tonduz 7865* (BR); N of Vara Blanca, *Croat 35622, 36048* (MO); Vara Blanca de Sarapiquí, *Skutch 3507* (MO, NY), *3593* (MICH, MO, NY); Volcán Barba near Sacramento, *Burger & Burger 7697, 9481* (MO); between Volcán Irazú & Volcán Barba, *Davidse & Pohl 1702* (MO). puntarenas & alajuela: Monteverde Nature Reserve, *Burger & Baker 9643* (MO). puntarenas: Cañas Gordas, *Pittier 11128* (BR); near Cotón, along Río Coto Brus, *Croat 26643, 26650A* (MO); W of Finca Las Cruces, *Luteyn 3847* (DUKE); vicinity of Monteverde, *Burger & Gentry 8567, 8672* (MO); *Luteyn 3400* (DUKE, MO); *Wilbur et al. 15810* (DUKE); *Wilbur 14260* (DUKE); SE of Santa Elena, *Almeda et al. 2035* (DUKE). san josé & heredia: slopes of Cerro Zurqui, *Almeda 3688* (CAS); Río Para Blanca, *Burger et al. 10268A* (MO). san josé: NW of Canaán, *Burger & Liesner 7086* (MO); NW of Cascajal, *Taylor & Taylor 11341* (NY); Cordillera Central above La Palma, *Luteyn 3307* (DUKE, MO); Copey, *Stork 1550* (MICH); La Palma, *Brenes 15055* (NY); *Tonduz 9698* (BR); between La Palma and La Hondura, *Luteyn 4255* (DUKE); Río Candelaria, *Tonduz 7893* (BR); Rió Naranjo, *Tonduz 7524* (BR); SW of San Isidro del General, *Croat 35265, 35300* (MO); N of San Jerónimo, *Utley & Utley 2894* (MO); Santa María de Dota, *Pittier 2339* (BR).

Guatemala. alta verapaz: Cobán, *Tuerckheim 1297* (BR, NY, US); Cubilhuitz, *Tuerckheim 8605* (NY, US); Finca Moca, *Johnson 143* (US); Pansamalá, *Tuerckheim 864* (P); SE of Tactic, *William et al. 40601* (F, MO, U). baja verapaz: vicinity Purulhá, *Croat 41177, 41284* (MO); *Tuerckheim 1768* (US). huehuetenango: N of Barillas, *Steyermark 48724* (F). san marcos: vicinity África, *Croat 40955* (MO); above Finca El Porvenir, *Steyermark 37975* (MO); La Trinidad, *Croat 40906* (MO); vicinity San Rafael, *Williams et al. 26202* (NY). zacapa: Mt. Virgen, *Steyermark 42870* (F).

Honduras. comayagua: El Achiote, *Yuncker 6270* (MO); vicinity Siguatepeque, *Molina 25472* (NY, US). la paz: near Cordillera Guajiquiro, *Molina & Molina 13885* (NY). morazán: Volcán de Guaimaca, *Molina 3184* (US). santa bárbara: E of Lake Yojoa, *Clewell & Hazlett 3882* (MO).

Mexico. chiapas: between Ixtapa & Pichucalco, *Croat 47798* (MO); vicinity Jitotol, *Breedlove 15432, 26088* (DS); vicinity Lake Montebello, *Croat 46677* (MO); *Miranda 2689* (MEXU); Munc. La Trinitaria, Montebello National Park, *Breedlove 35120, 38797* (DS); Munc. Ocosingo, *Dressler 1517* (MEXU, MICH, US); near Pueblo Nuevo Solistahuacán, *Raven & Breedlove 20025* (DS); *Thorne & Lathrop 6505* (RSA); *Lathrop 6509* (RSA); *Thorne & Lathrop 40280* (DS, LL, RSA); E of Río Napac, *MacDougall 6894* (MEXU); SW slope of Volcán Tacaná, *Breedlove 42509* (DS); *Croat 47180* (MO). oaxaca: vicinity Ixtlán de Juárez, *McAlpin 1048* (DUKE); Sierra de Juárez, *Croat 39816* (MO); between Tuxtepec & Oaxaca, *Croat 48067* (MO); Vista Hermosa, *Moore & Bunting 8922* (BH).

Nicaragua. jinotega: NW of Aranjuez, *Stevens 9173* (MO); near Cerro Chimborazo, *Atwood A221* (MO); *Neill N163* (MO); Matagalpa: Highway 3 from Jinotega to Matagalpa, *Croat 43069, 43106* (MO); N of Matagalpa, *Croat 43114* (MO); above Santa María de Ostuma, *Molina 20382* (NY); *Molina & Molina 30538* (MO); *Neill 1575* (MO); *Williams et al. 27592, 27724* (MO); El Porvenir, *Molina 20545* (MO). zelaya: vicinity Cerro Saslaya, *Neill 3812, Stevens 6713* (MO)

Anthurium montanum Hemsl., Diagn. Pl. Nov. Mexic. 36. 1878. Type: Guatemala, Volcán de Fuego, above Calderas at 2,700 m, *Salvin* (K).

Usually epiphytic, stems 5–15 cm long, 2.5–7 cm diam.; leaf scars 2.5 cm wide; roots numerous, thick, descending; cataphylls coriaceous, 6–12 cm long, rounded at apex with subapical apic-

ulum, ca. 3 mm long, drying reddish-brown (B & K Yellow-red 5/7.5) usually persisting as fibers around stem. LEAVES with petioles spreading to erect, (6.5)22–75(99) cm long, 5–15 mm diam., usually D-shaped, sometimes subterete, broadly sulcate, the margins acute; geniculum 1.5–3 cm long (sometimes tinged with red in larger plants); blades triangular to ovate, subcoriaceous, gradually to abruptly acuminate at apex, broadly to deeply lobed at base, 12–55 cm long, 7–30 cm wide, broadest at base; the anterior lobe 11–40 cm long; posterior lobes 5.5–18.5 cm long, usually directed upward; the sinus rarely arcuate, usually hippocrepiform or spathulate, rounded at apex; the upper surface semiglossy to glossy, the lower surface semiglossy; the midrib broadly raised at base above, acutely raised to middle, sunken at apex, convexly raised below; basal veins 3–7 pairs, the fourth to seventh coalesced 1–5.5 cm, raised above and below; the posterior ribs naked, the outer margin rolled up; primary lateral veins 6–11 per side, departing the midrib at 45°–60° angle; weakly sunken above, raised below, straight to the collective vein; lesser veins sunken above, raised below; collective vein arising from the first basal vein, sunken above, raised below, 5–14 mm from margin. INFLORESCENCE spreading, shorter than or equalling leaves; peduncle 17–49(65) cm long, 3–8 mm diam., terete to weakly ribbed, shorter than petioles; spathe subcoriaceous, yellow-green to medium green, tinged with red-violet (B & K Yellow-green 6/7.5 to 5/10), narrowly ovate to lanceolate, 6–8.5 cm long, 1.5–2.7 cm wide, broadest just above point of attachment, caudate-acuminate at apex, round to cordate at base, inserted at 90° angle on peduncle; stipe 2.5 cm long, 4 mm diam., yellow to medium green; spadix green tinged with purple, deep purple or brown, 4–20 cm long, 5–11 mm diam. at base, 4–8 mm diam. at apex; flowers rhombic to sub-4-lobed, 2.5–4.2 mm long, 2.6–4 mm wide, the sides straight to sigmoid; 5–9 flowers visible in the principal spiral, 5–6 flowers visible in the alternate spiral; tepals matte with pale punctations, minutely and densely papillate, droplets sparse; lateral tepals 1.5–2.5 mm wide, the inner margins convex to straight and turned up against pistil; pistils weakly emergent, green; stigma linear, 0.5–0.7 mm long; stamens developing promptly from the base, the full complement developed promptly, the leading stamens preceding alternates only by 2 or 3 spirals; anthers cream to tan, 0.2 mm long, 0.5 mm wide, exserted on short, transparent filaments, quickly retracting; thecae oblong-ellipsoid, slightly divaricate; pollen yellow to cream, fading to white. INFRUCTESCENCE pendent; spadix to 20 cm long, to 2 cm diam.; berries oblong to obtusely triangular, truncate and usually broadest at apex, medium orange (B & K Yellow-red 7/2.5), 10–13 mm in both directions; mesocarp firm, thick with few raphide cells; seeds 1–2, pale greenish-white, weakly flattened, ± reniform, 5–7.5 mm long, 4–6 mm wide, 3–4 mm thick, minutely appendaged at both ends. Figs. 111, 112, and 113.

Anthurium montanum is known only from southeast Chiapas and southwest Guatemala at elevations of 1,200 to 2,900 m in wet mountain forests and cloud forests (not designated as part of the Holdridge Life Zone system). In Chiapas the species is known principally from "bosque de oyamel" but probably also "bosque pino-encino." The type locality of *A. montanum,* namely Volcán de Fuego, is located in southwest Guatemala along the frontiers of the departments of Escuintla, Chimaltenengo, and Sacatepéquez. According to annotations by N. E. Brown on the type collection, it consists of a mixed collection of two species, namely *A. andicola* and *A. montanum.* Despite my reluctance to question the generally excellent observations of Brown, I can see no differences in the two parts of the collection and certainly one part does not appear to be *A. andicola.*

The species is in section *Belolonchium* and is recognized by its narrowly ovate blades, its usually D-shaped, weakly glaucous petioles, long-pedunculate inflorescences with a matte, green to violet-purple spadix, and thin dilacerating cataphylls.

Anthurium montanum is confused with *A. huixtlense,* a more wide ranging species usually occurring from about 300 to 1,500 m (to 1,800 m fide *Flora of Guatemala*). The latter species is distinguished from *A. montanum* by having coriaceous cataphylls that turn reddish-brown and persist intact, and by having a reddish-violet to lavender, rarely white spadix with glossy tepals. In *A. montanum* the cataphylls are thin and soon weather to slender fibers while the tepals are matte and either green or violet-purple.

Anthurium montanum is also similar to *A. umbrosum,* a species from northern Oaxaca with similar narrowly ovate leaf blades and dilacerating cataphylls, but that species differs in having

FIGURES 112–115. 112. *Anthurium montanum* Hemsl., *Croat 41015*.—113. *Anthurium montanum* Hemsl., *Croat 47235*.—114–115. *Anthurium nakamurae* Matuda. *Croat 47407*.

a terete petiole and a leaf blade that is relatively straight along the margin.

Anthurium montanum is perhaps most closely related to *A. titanium*, a species from southeast Chiapas and adjacent parts of Guatemala and sympatric with *A. montanum* in the lower parts of its elevational range (i.e., below 1,800 m). The two species share a D-shaped, weakly glaucous petiole and leaf blades of similar color and texture, but those of *A. titanium* attain generally much larger size and are almost round to broadly ovate in outline, while those of *A. montanum* are generally narrowly ovate.

Another species with which *A. montanum* can be confused is *A. chamulense*, with which it is sympatric in eastern Chiapas. They share a similar blade shape but the latter species is distinguished by having blades more coriaceous.

Anthurium montanum is apparently closely related to *A. cordatotriangulum*, which differs in having a more deltoid leaf blade with conspicuously elevated veins, a generally longer and broader spathe, and a longer, more tapered spadix. Both species have been collected near Rosario south of Motozintla, but the only species apparently now occurring in the area is *A. montanum*.

GUATEMALA. CHIMALTENANGO: no other location, *Standley 62304* (F); above Las Calderas, *Standley 80173, 80174, 80190, 87845* (F). HUEHUETENANGO: below La Libertad, *Standley 51172* (F). QUEZALTENANGO: S of San Martín, *Standley 83836, 84991* (F); Volcán de Zunil, *Standley 65381* (F); above Zunil, *Standley 85778, 85821* (F). ESCUINTLA: above Calderas, Volcán de Fuego, *Salvin s.n.* (K). RETALHULEU: Volcán Pacaya, *Harmon 4176* (UMO). SAN MARCOS: vicinity San Pedro, *Almeda 3460* (DUKE); vicinity San Marcos, *Croat 41015* (MO); San Pedro, *Steyermark 47217* (F, NY); Sierra Madre Mountains, W of San Marcos, *Williams et al. 27214* (F); west of San Pedro Sac, *Luteyn & Almeda 3460* (DUKE, MO); vicinity San Rafael, *Standley 86482, 86529* (F); *Williams et al. 26010* (NY, US); Volcán Tajumulco, *Steyermark 37063* (F). SUCHITEPÉQUEZ: Volcań Santa Clara, *Steyermark 46684, 46751* (F); Mazatenango, *Tejada 308, 310* (US).

MEXICO. CHIAPAS: vicinity El Rosario, *Croat 40751, 47235* (MO); Escuintla, Monte Ovando, *Matuda 2571* (MEXU, MICH); *Matuda 4212* (DS, MEXU, MICH, NY, UC); *Matuda 4219, 19663* (MEXU); *Matuda 17744* (F, MEXU); *Matuda 18167* (MEXU, NY); La Grandeza, *Matuda 5604* (F, MEXU, MO); Mt. Pashtal, *Matuda 17971* (MEXU); Motozintla, *Breedlove 25786, 41725* (DS); San Luis, Siltepec, *Matuda 18276* (MEXU); Saxchanal, *Matuda 17805* (MEXU); E side of Volcán Tacaná, *Breedlove 31706* (DS); *Croat 47161* (MO).

Anthurium monteverdense Croat & Baker, Brenesia 16 (Supl. 1): 62. 1979. TYPE: Costa Rica. Puntarenas: Monte Verde Biological Preserve (operated by the Tropical Science Center), *Kennedy 582* (F, holotype).

Epiphyte, to 1.5 m tall; stems thick, moderately short, the internodes very short; cataphylls thick, persistent, drying reddish-brown. LEAVES with petioles terete, 29–50 cm long, 6–8 mm diam.; geniculum moderately obscure, to 4 cm long; blades coriaceous, ovate, broadest just below the middle, acuminate and downturned at apex, conspicuously lobed at base, 29–50 cm long, 18.5–34 cm wide; the anterior lobe 22–36 cm long, the margins broadly convex; the posterior lobes 7–12 cm long; sinus spathulate to hippocrepiform, longer than broad, rounded at apex; upper surface semiglossy with sparse, ± obscure, raphide cells, lower surface sparsely and obscurely dark dotted; the midrib raised above and below; primary lateral veins 3–5 per side, departing midrib at 40°–50° angle, ± straight until near the margin, then prominently arcuate-ascending and joining the margin; basal veins 5–6 pairs, 2–4 of them coalesced 1.5–4 cm, arcuate and joining the margin, ± loop-connecting the secondary veins; posterior rib prominently curved, naked for most of its length, turned up along its outer margin; collective vein arising from the uppermost 1 or 2 primary lateral veins. INFLORESCENCE shorter than leaves; peduncle 35–40 (100) cm long, 6–8 mm diam.; spathe coriaceous, white, broadly ovate, 8–10(17.5) cm long, 5–6 (8.5) cm wide, acuminate-cuspidate at apex, rounded at base, broadest at or slightly below middle, held erect, inserted at ca. 45° angle on peduncle; spadix green to creamy yellow or yellowish-tan, 5.5–14.5 cm long, 1–2.2 cm diam.; flowers rhombic to weakly 4-lobed, 2–2.2 mm long, 2.2–2.5 mm wide (dry); 10–12 flowers visible in either spiral; the lateral tepals 1.2–1.3 mm long, the inner margin broadly convex; pistil and stamens not studied. INFRUCTESCENCE not seen.

The species is apparently endemic to the mountains in west central Costa Rica at elevations of 1,400 to 1,600 m, in the Provinces of Alajuela and Puntarenas in lower montane moist and premontane wet forest.

Anthurium monteverdense belongs in the section *Calomystrium* and is closely related to *A. hoffmannii*, but that species differs in having an ovate-lanceolate spathe.

COSTA RICA. ALAJUELA: W of Monteverde Reserve, *Dryer 1529* (F); Zapote, *Austin Smith 2893* (F); Zarcero, *Austin Smith H564* (F). PUNTARENAS & ALAJUELA:

Monteverde Reserve, *Burger & Baker 9710* (MO); *Kennedy 582* (MO).

Anthurium nakamurae Matuda, Revista Soc. Mex. Hist. Nat. 11: 93, Fig. 2. 1950. TYPE: Mexico. Chiapas: Cascada, Siltepec, elev. 1,200 m, June 2, 1949. *Matuda 18668* (MEXU-85863, holotype).

Epiphyte; stems very short; roots thick, green, descending; cataphylls subcoriaceous, 4–6 cm long, tinged red-violet, acuminate at apex with short subapical apiculum, drying medium brown (B & K Yellow 4/2.5), weathering into reticulate fibers. LEAVES erect to spreading; petioles 10.5–40 cm long, 4–5 mm diam., usually terete, sometimes subterete to weakly sulcate; geniculum 1.5–2 cm long; blades lanceolate to narrowly triangular, acuminate at apex, truncate to weakly lobed at base, 14.5–45 cm long, 4.5–12 cm wide, broadest at middle or just above; the anterior lobe 15–42 cm long, the margins straight, sometimes convex in apical one half of blade; posterior lobes 2–5 cm long; sinus arcuate with petiole decurrent to parabolic; both surfaces semiglossy; midrib flat at base above, raised near middle, sunken at apex, raised below; basal veins 2–3 pairs, free to base, flat and ± obscure above, prominulous below; primary lateral veins 10–12 per side, departing midrib at 30° angle, flat and ± obscure above, flat to prominulous below; lesser veins obscure above and below; collective vein usually arising from the first or second basal vein, sometimes from one of the primary lateral veins near the base, flat above, prominulous below, 3–5 mm from the margin. INFLORESCENCE spreading, equal to or longer than leaves; peduncle 30–47 cm long, 3–5 mm diam.; spathe thin, lanceolate to narrowly ovate, green heavily tinged red-violet, 4.5–6 cm long, 1.9–2.5 cm wide, long-acuminate at apex, weakly cordate at base, inserted at 90° angle on peduncle; spadix sessile or stipitate, the stipe sometimes to 1 cm (rarely to 4 cm long), olive-green or purple, 3.5–8.2 cm long, 6–7 mm diam. at base, 3–5 mm diam. at apex; the flowers 4-lobed, 3.2–3.5 mm long, 2.6–3.3 mm wide, the sides sigmoid; 5–6 flowers visible in the principal spiral, 8–10 flowers visible in the alternate spiral; tepals matte, densely papillate, lateral tepals 1–1.6 mm wide, the inner margin convex, turned up, the outer margins tinged red-violet; pistils emergent, red-violet; stigma linear, ca. 0.2 mm long, scarcely open; stamens developing rapidly from the base, the laterals first, followed quickly by the alternates, the leading stamens emerging only 1–2 spirals ahead of the third and fourth stamens; anthers pale yellow, 0.6 mm in both directions, held over pistil, retracting to edge of tepals but not contiguous; thecae ellipsoid, scarcely divaricate; pollen bright yellow, fading to white. INFRUCTESCENCE pendent; spathe persistent; spadix to 17 cm long; berries red, obovoid, round at apex, ca. 10 mm long, 7 mm wide; seeds 2, pale green, flattened, 5–6 mm long, ca. 3 mm wide. Figs. 114 and 115.

Anthurium nakamurae is apparently endemic to eastern Chiapas in the vicinity of Siltepec and La Grandeza at elevations of 1,200 to 2,100 m. My collection was made in a cloud forest area that appeared to be either tropical wet forest or premontane rain forest.

The species is a member of section *Belolonchium* and is characterized by its usually subterete, sometimes weakly sulcate petiole, its moderately thick, oblong to oblong-elliptic leaf blade, which is usually truncate (rarely subcordate) at the base and usually broadest above the base. Blades are often weakly constricted somewhat above the base.

Anthurium nakamurae is most similar to *A. parvispathum,* which has leaf blades oblong to oblong-elliptic with the base rounded to truncate, but that species differs in having much thicker blades that are generally much paler and matte on the lower surface. Moreover, typical *A. parvispathum* is usually found growing on rocks while *A. nakamurae* is reported principally epiphytic and, where I have seen it, grows high up in trees.

Two collections made by *Breedlove* (*31955* and *40413*) vary somewhat in the thickness of the blade and in having relatively longer cataphylls that appear to persist intact rather than weather to reticulate fibers as in typical *A. nakamurae.*

MEXICO. CHIAPAS: vicinity Siltepec on road to Huixtla, *Breedlove 31955, 40413* (DS); vicinity Motozintla and Siltepec, *Croat 47407, 47419, 47461* (MO); Cascada, Siltepec, *Matuda 18668, 19660* (MEXU); La Grandeza, *Matuda 5576* (F, MEXU).

Anthurium nelsonii Croat, sp. nov. TYPE: Mexico. Oaxaca: Reyes (Reyes Etla, NNW of city of Oaxaca) 2,500–3,466 m; *E. W. Nelson 1758* (US-358640, holotype).

Planta terrestris, ca. 1 m alta; caudex ca. 4 cm diam.; petiolus 29–48 cm longus, sulcatus late acuteque; lamina ovata aut triangularis-ovata, 30–57 cm longa, 22–56 cm lata, basi cordata profunde, in pagina inferiore albida hebetataque; inflorescentia effusa-pendula; pe-

dunculus 30–43 cm longus; spatha viridis, 10–13 cm longa, 1.5–3 cm lata; spadix purpureus, 6.5–15 cm longus; baccae obovoideae.

Terrestrial, less than 1 m tall; stems ca. 4 cm diam.; roots 3 mm diam.; tan, smooth to woolly pubescent (dry); cataphylls ca. 8 cm long, drying tan to reddish-brown, weathering to moderately thin fibers. LEAVES with petioles 29–48 cm long, 6–8 mm diam., sharply and broadly sulcate adaxially; the geniculum 1–1.5 cm long; blades broadly ovate to ovate-triangular, 30–57 cm long, 22–56 cm wide, broadest at base, acute to narrowly rounded and apiculate at apex, deeply lobed at base, the margin sinuate and undulate; anterior lobe 25–45 cm long; posterior lobes 11.5–25 cm long from apex of sinus to the outermost point; the sinus arcuate or arcuate with petiole decurrent; upper surface semiglossy, lower surface matte, often whitish with glistening translucent circular cells scattered in the epidermis (visible at high magnification on dried leaves); midrib convexly raised above; the basal veins 5–9, all except the first and second (third) coalesced 5–11.5 cm, raised on both surfaces, drying darker than the surface; posterior ribs broadly arcuate, naked most their length; primary lateral veins 5–9 per side, almost straight or gradually curved upward, arcuate-ascending near margin and joining margin, raised on both surfaces; collective vein arising from one of the lowermost primary lateral veins (rarely as low as the first basal vein), 3–7 mm from margin, weakly raised on both surfaces. INFLORESCENCE spreading-pendent (?); peduncle 30–43 cm long, 3–5 mm diam., terete, shorter to longer than petioles; spathe subcoriaceous, green, lanceolate to ovate-lanceolate, 10–13 cm long, 1.5–3 cm wide, broadest just above base, narrowly acuminate at apex, rounded to subcordate at base, inserted at ca. 45° angle on peduncle; the stipe 3–25 mm long in back, 1–15 mm long in front, 3–4 mm diam.; the spadix violet-purple, 6.5–15 cm long, 6–9 mm diam. at base, 4–5 mm diam. at apex, sometimes curved; the flowers rhombic, 3.6–4.7 mm long, 2.6–3.9 mm wide (dry), the sides scarcely to jaggedly sigmoid; 6–8 flowers visible in the principal spiral, 4–6 flowers visible in the alternate spiral; tepals matte, very minutely papillate, lateral tepals 2.7–3 mm wide, the inner margin broadly rounded; pistils not emergent; stigma oblong, 1 mm long; stamens emerging from the base in a moderately slow progression; the anthers held in a close cluster completely obscuring the pistil, ca. 1 mm long, ca. 1.4 mm wide; thecae narrowly ovate, scarcely divaricate; pollen not seen. INFRUCTESCENCE pendent, berries often developing only in the basal one half or one third; spathe persistent; spadix ca. 20 cm long, 3 cm diam.; berries obovoid, truncate to broadly rounded and scurfy, 10–13 mm long, 9–10 mm diam.; pericarp moderately thick, leathery at apex, small raphide cells, very dense in lower three quarters of berry; seeds 1–2, ± lens-shaped, brown, considerably flattened, raphide cells sparse and minute, 9–13 mm long, 7–9 mm wide, 3–4 mm thick, weakly depressed at apex, with a sticky, gelatinous appendage sometimes as large as seed. Figs. 117 and 118.

Anthurium nelsonii is endemic to Mexico, occurring in the State of Oaxaca in the arid region north northeast of the city of Oaxaca between latitudes 17°10′N and 18°N at elevations of 1,000 to 2,500 m. The principal vegetation types of the region are "selva baja caducifolia" and "bosque pino-encino."

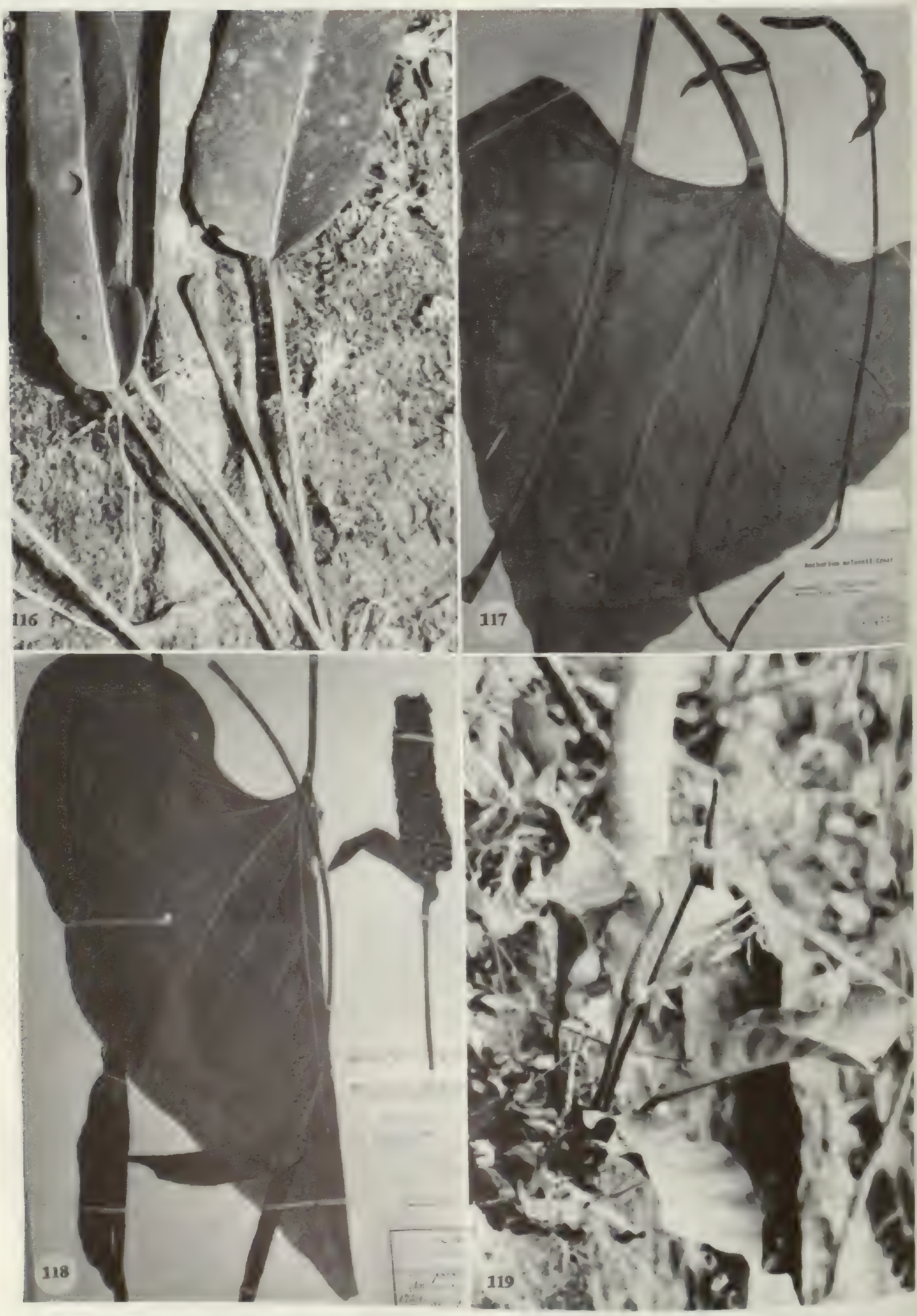
The species is named in honor of the first collector, E. W. Nelson, who made the first collections in 1894. The collections have in part been confused with *A. andicola,* a species occurring in wetter parts of northern Oaxaca.

Anthurium nelsonii is a member of section *Belolonchium* and is distinguished by its broadly ovate-triangular blade with well developed posterior lobes and a broad sinus and by its sharply and broadly sulcate petiole. The most characteristic feature and the principal feature by which it is distinguished from *A. andicola* is its matte, often whitish lower blade surface. The latter species is semiglossy on the lower surface.

MEXICO. OAXACA: no other location, *Conzatti 1724* (US); Mirador, *Ernest 2500* (US); Oaxaca City, *Nelson 1758* (US); Santa Catarina Cañon, *Conzatti & Gonzalez 1180* (GH); vicinity Telixtlahuaca, *Delgadillo 225* (MEXU); Tomellín Cañon, *Rose & Rose 11351* (NY, US).

Anthurium nizandense Matuda, Bol. Soc. Bot. México 24: 35, Fig. 1. 1959. TYPE: Mexico. Oaxaca: Nizanda near the Isthmus of Tehuantepec (16°40′N, 95°2′W) dry, rocky hill, *MacDougall s.n.* (January 6, 1959) (MEXU, holotype).

Anthurium kruseanum Matuda, Anales Inst. Biol. Univ. Nac. México 36: 107, Fig. 1. 1966. TYPE: Mexico. Guerrero: La Junta (at junction of Río Omitlán and Río Papagayo) south of Tierra Colorada, on rocks in shade, *Hubert Kruse 881* (MEXU, holotype).



FIGURES 116–119. 116. *Anthurium nakamurae* Matuda, *Croat 47407*.—117–118. *Anthurium nelsonii* Croat, *Rose & Rose 11357* (Type).—119. *Anthurium nizandense* Matuda, *Croat 45756*.

Usually terrestrial or epipetric; stems thick; leaf scars 0.7–1.2 cm long; roots numerous, thick, tan; cataphylls subcoriaceous, 3–7 cm long, rounded and minutely apiculate at apex, drying dark brown, persisting intact at apex, weathering to reticulate fibers at base. LEAVES erect-spreading; petioles 6–15 cm long, 5–6 mm diam., subquadrangular to subterete, broadly and sharply sulcate, sometimes tinged with red-violet; geniculum 1–1.5 cm long; blades narrowly obovate to obovate-elliptic, subcoriaceous, 25–36.5 cm long, 10.7–18 cm wide, broadest just above middle, acute at apex and base (the tip glandular); the upper surface matte to semiglossy, the lower surface matte, both surfaces having short, linear raphide cells, the epidermal cells mounded (i.e., raised and convex); the midrib acutely raised above, convexly raised below; primary lateral veins 6–8 per side, departing midrib at 50°–60° angle, prominent above and below; straight to weakly arcuate-ascending to collective vein; lesser veins scarcely visible and flat on both surfaces; collective vein arising from one of the primary lateral veins near middle of blade, 3–9 mm from margin, loop-connected with the remaining primary lateral veins. INFLORESCENCE erect, equalling or longer than leaves; peduncle 31–55 cm long, 5–8 mm diam., terete; spathe subcoriaceous, green, ovate-lanceolate, ca. 8 cm long, 2.5 cm wide, broadest near the base, inserted at 45° angle on peduncle; spadix pale green becoming reddish-brown, 12–14 cm long, 9–11 mm diam. at base, 4 mm diam. at apex; the flowers rhombic, 1.8–2.5 mm long, 2.8–3 mm wide, the sides sigmoid; 7–9 flowers visible in the principal spiral, 5–6 flowers visible in the alternate spiral; lateral tepals 1.5 mm wide, broadly rounded to weakly concave; the pistils not emergent; stigmas broadly ellipsoid; stamens emerging in a prompt, complete sequence, held just above tepals in a contiguous circle around stigma; anthers ca. 0.4 mm long, 0.6 mm wide; thecae ellipsoid, weakly divaricate. INFRUCTESCENCE pendent; the spathe withered; spadix 6.5 cm long, 1.5 mm wide; berries round, greenish-white, 8 mm long; mesocarp transparent, juicy, pulpy; seeds 1 (2?) per berry, broadly obovoid, pale yellow (B & K Yellow 9/2.5), tinged with brown at base and on one side, 5.2–5.4 mm long, 4.5–4.7 mm wide, 3.4–4 mm thick, enveloped by a gelatinous sack; appendage minute, translucent, ± gnarled at apex on side, tinged with brown. Figs. 119 and 120.

Anthurium nizandense is endemic to Mexico in southern Guerrero and southern Oaxaca, where it occurs at less than 850 m in seasonally very dry habitats on steep, rocky cliffs. It is known only from the vicinity of Tierra Colorada in Guerrero and at Nizanda in Oaxaca.

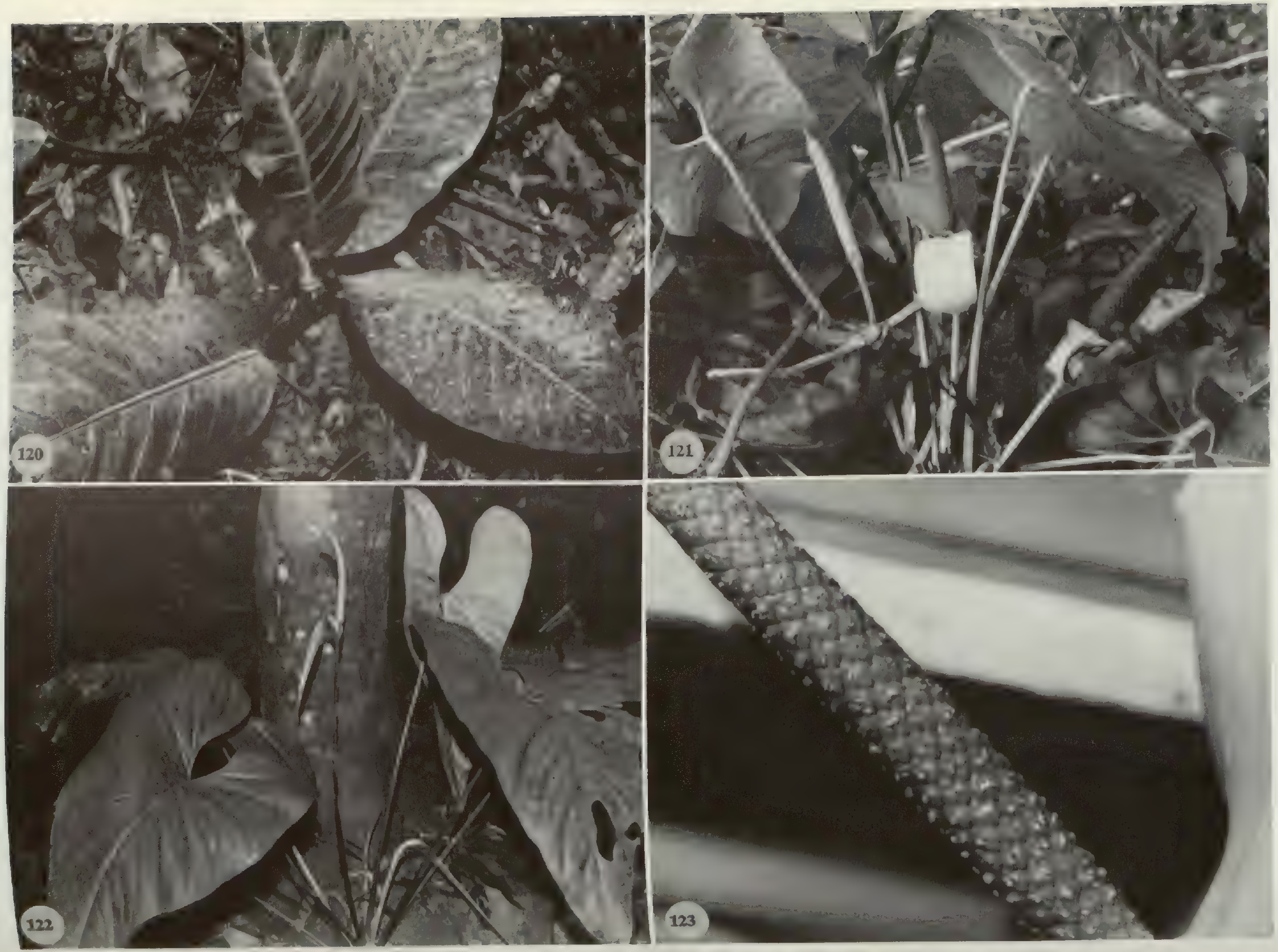
The species is a member of section *Pachyneurium* and is recognized by its greenish-white berries and by its thick, narrowly to broadly elliptic or oblanceolate-elliptic, relatively long-petiolate leaves that are matte on the lower surface and sometimes exhibit a dense array of minute, linear raphide cells on drying. It has at least the lower primary lateral veins extending to the margin. Matuda reported the petiole to be subquadrangular, but this was possibly due to a misinterpretation of the dried specimen since this character is not apparent on the live material. The epidermal cells on both surfaces of the blade are convexly raised.

In the area of Mexico where it occurs, *A. nizandense* could be confused only with *A. schlechtendalii* ssp. *jimenezii,* which is more generally abundant and occurs in similar habitats. *Anthurium nizandense* is distinguished by its proportionately longer petioles and its more typically elliptic blade, which is distinctly matte on the lower surface. In *A. nizandense* the blades are 1.3–2.5 times longer than the petioles. In *A. schlechtendalii* ssp. *jimenezii,* the leaf blades are usually semiglossy beneath and usually 6–10 times longer (rarely as little as 3 times longer) than the petiole.

MEXICO. GUERRERO: between bridge over Río Omitlán & confluence of Río Papagayo, *Croat 45756* (MO); Tierra Colorada, *Kruse 1595* (MEXU). OAXACA: Nizanda near Isthmus of Tehuantepec, *MacDougall s.n.* (MEXU).

Anthurium obtusilobum Schott, Oesterr. Bot. Z. 8: 181. 1858. TYPE: Costa Rica, near San Miguel, *Wendland 777* (GOET, holotype; W, isotype).

Epiphyte or terrestrial; stems ca. 1.5 cm thick, to 30 cm long; roots numerous, moderately thin; cataphylls 10–15 cm long, drying tan, persisting intact. LEAVES with petioles ± erect, subterete, obscurely sulcate, 19–60 cm long, 6–9 mm diam.; geniculum ca. 2 cm long; blades ovate, moderately thick, 15–46 cm long, 9.5–28 cm wide, gradually to abruptly acuminate at apex, deeply lobed at base; anterior lobe 21–33 cm long, the



FIGURES 120–123. 120. *Anthurium nizandense* Matuda, *Croat 45756*.—121. *Anthurium obtusilobum* Schott, *Croat 49997*.—122. *Anthurium ochranthum* C. Koch, *Croat 4569*.—123. *Anthurium ochranthum* C. Koch, *Croat 33965*.

margins convex; posterior lobes 9–16 cm long; sinus spathulate, rounded at apex; both surfaces matte; midrib convexly raised at base above, narrowing and acute at apex, raised below; primary lateral veins 3–6 per side, departing midrib at 45° angle, raised above and below; lesser veins sunken above, raised below; basal veins ca. 8 pairs, 3–4 coalesced 2.5–4 cm; posterior ribs naked, turned up along the outer margin; collective vein arising from one of the lowermost basal veins, extending to apex, 3–7 mm from margin. INFLORESCENCE spreading, shorter than leaves; peduncle (7)15–43 cm long, shorter than petioles; spathe oblong-elliptic, pale green to white, 7–11.5 cm long, 2.3–2.7 cm wide, long-acuminate at apex, obtuse at base; spadix cream to pale yellow-green, turning dark lavender to violet-purple, weakly tapered at apex, 4.5–7.6 cm long, 8–11 mm diam. at base, 5–7 mm diam. at apex; the flowers 4-lobed, ca. 3 mm long, ca. 4 mm wide, the sides jaggedly sigmoid; 5–10 flowers visible in the principal spiral, 8–9 flowers visible in the alternate spiral; tepals glossy, lateral tepals ca. 1.8 mm wide, the inner margin upturned; pistils raised, white to pale green; stigma brushlike, 0.4–1 mm long, glistening papillae exserted 4–5 days before first stamens emerge, turning brown; stamens emerging slowly from base, exserted on short white filaments, held over and obscuring pistil; anthers white, 0.3–0.5 mm long, 0.3–0.9 mm wide; thecae ellipsoid, not divaricate; pollen white. INFRUCTESCENCE with spadix to 15 cm long; berries red-violet, ovate, acute at apex; seeds not seen. Fig. 121.

Anthurium obtusilobum ranges from Costa Rica to Colombia (Chocó) at elevations of 600 to 1,550 m in premontane wet, tropical wet, premontane rain, and lower montane wet forest.

The species is in section *Calomystrium* and is closest to *A. hoffmannii*, sharing with that species thick, persistent, reddish-brown, entire cataphylls and a similar inflorescence. It is readily separated from other members of the section by having the collective vein arising from one of the lowermost basal veins and continuing to the apex close to the margin.

COSTA RICA. Near San Miguel, *Wendland 777* (GOET). ALAJUELA: NW of Cariblanco, *Luteyn 3222* (DUKE); *3341* (DUKE, MO); W of Fortuna, NW of Volcán Arenal, *Taylor & Taylor 11585* (MO); between Naranjo & Aguas Zarcas, *Croat 46953* (MO); between Naranjo & Quesada, N of Zapote, *Croat 46920* (MO); vicinity San Ramón, *Almeda & Nakai 3849* (CAS); *Primack & Luteyn 374* (DUKE); *Utley & Utley 4582* (DUKE, MO); vicinity of Vara Blanca, *Luteyn 3906* (DUKE); San Luis de Zarcero, *Smith 1259* (NY); vicinity Zarcero, *Smith 4991* (MO). CARTAGO: E of Cachí, *Croat 47081* (MO); Muñeco *Standley & Torres 51712* (US); near Selva above Río Taus, *Taylor & Taylor 11436* (NY); near Tapantí, *Lent 27* (DAV, NY); SE of Tapantí, *Lent 840* (NY, US, WIS); road from Tapantí to Taus, *Utley & Utley 5593* (DUKE); NE of Turrialba, *Croat 43356, 43358* (MO). HEREDIA: N of Vara Blanca, Vicinity Río La Paz Grande, *Croat 36024* (MO). LIMÓN: Toro Amarillo, *Tessene 1422* (WIS). PUNTARENAS: Las Cruces Botanical Garden, *Croat 32966* (MO). SAN JOSÉ: Laguna la Chonta, *Standley 42358* (US); La Palma, *Luteyn 2999* (DUKE).

Anthurium ochranthum C. Koch, Ind. Sem. Hort. Berol. App. 6. 1853. TYPE: Costa Rica, *Wendland s.n.* (P, hololectotype; B, BP, LE, W, isolectotypes; designated Croat & Baker, 1979).

Anthurium lapathifolium Schott, Oesterr. Bot. Wochenbl. 7: 309. 1857. TYPE: Panama, *Fendler 429* (K).

Anthurium triangulum Engl., Bot. Jahrb. Syst. 25: 383. 1898. TYPE: Costa Rica. Limón: Talamanca, in forest near Shirores, 100 m elev., *Pittier & Tonduz 9225* (B).

Anthurium tsakianum Engl., Bot. Jahrb. Syst. 25: 423. 1898. TYPE: Costa Rica, Talamanca, in forest near Tsakí, 200 m elev., *Tonduz 9510* (B, holotype; CR, isotype).

Anthurium baileyi Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 66. 1940. TYPE: Panama. Canal Zone: Barro Colorado Island, *Bailey & Bailey 196* (F, holotype).

Terrestrial, rarely more than 1.5 m tall; stem to 45 cm long, 2–4 cm diam.; cataphylls 11.5–13 cm long, drying brown, weathering to coarse linear fibers. LEAVES erect-spreading; petioles terete or obscurely sulcate, 30–70(90) cm long, 5–8 mm diam., blades ovate-triangular, moderately thin, 39–75 cm long, 18–48 cm wide, acuminate at apex, deeply lobed at base; the anterior lobe 23–52 cm long; posterior lobes 11–22 cm from sinus to outermost point; sinus narrowly triangular; the upper surface matte to semiglossy, the lower surface matte; the midrib raised above and below; primary lateral veins 4–6, raised in valleys above, raised below; collective vein arising from the uppermost basal vein. INFLORESCENCE erect, usually shorter than or sometimes longer than leaves; peduncles 24–63 cm long; spathe, green or pale green sometimes tinged with red-violet, lanceolate, 10–15(32) cm long, 3–5 cm wide; spadix green turning bright yellow, 7–22 cm long, 5–8 mm diam. at base, 4–6 mm diam. at apex; flowers 4-lobed, ca. 2.6 mm long

(dry), ca. 2.3 mm wide (dry), the sides jaggedly sigmoid; ca. 6 flowers visible in the principal spiral, ca. 9 flowers visible in the alternate spiral; tepals glossy, lateral tepals 1.7–2 mm wide, the inner margin convex; pistil weakly emergent, green; stigma brushlike; stamens emerging scattered throughout length of spadix, usually the lateral stamens first, the alternates quickly following; anthers held over pistil; thecae yellow-orange; pollen orange. INFRUCTESCENCE with spadix 11–24 cm long; berries violet-purple at apex, white at base, obovoid, 7–9 mm long. Figs. 122 and 123.

Anthurium ochranthum is known from Costa Rica to Panama from sea level to 1,350 m, most commonly in tropical wet forest but also in wetter parts of tropical moist forest and in premontane wet and premontane rain forest.

The species is placed in section *Belolonchium* and is recognized by its terrestrial habit, bright yellow, long-tapered spadix, violet-purple and white berries, and the leaf blades that have the anterior lobe sometimes concave along the margins. It is most closely related to *A. pluricostatum.* See the discussion following that species for differences.

COSTA RICA. ALAJUELA: NNE of Bijagua, *Croat 36285, 36471* (MO); between Naranjo & Aguas Zarcas, *Croat 46951* (MO); near Río Segundo, *Croat 36857* (MO). CARTAGO: SE of Platanillo, *Croat 36809, 36733* (MO). GUANACASTE: Volcán Miravalles, *Burger & Gentry 9100* (MO). LIMÓN: between Siguerres & Río Pacuare, *Burger & Liesner 6880* (MO, NY).

Anthurium oerstedianum Schott, Oesterr. Bot. Z. 8: 180. 1858. TYPE: Costa Rica, near Naranjo, *Oersted s.n.* (W, destroyed?; Photo of Schott Aroid Drawing #228, NYBG Neg. #N.S. 3817).

Anthurium cuspidifolium Schott, Oesterr. Bot. Z. 8: 180. 1858. TYPE: Costa Rica, *Oersted s.n.* (W, destroyed?; Photo of Type at W, Field Mus. #29812 (MO); Photo of Schott Aroid Drawing #314, NYBG Neg. #N.S. 3816).

Terrestrial; stems short, to 2 cm diam.; roots numerous, short, tan; cataphylls 7–12 cm long, moderately thin, apiculate at apex, drying brown, persisting intact, ultimately deciduous. LEAVES usually ± erect; petioles ± quadrangular, (12)30–65 cm long, ca. 0.6 cm wide; the geniculum 1.5–2 cm long, remote from base of blade 10–20 cm; blades ovate to narrowly ovate or lanceolate-elliptic, moderately thin, 20–66 cm long, 8.5–30 cm wide, caudate-acuminate at apex, obtuse to truncate, sometimes rounded to subcordate at base, abruptly decurrent on petiole; both surfaces semiglossy; midrib convexly raised above, raised and obscurely ribbed below; primary lateral veins 11–20 per side, raised in valleys above, raised below; lesser veins sunken above, obscure below; collective vein arising from one of the lowermost primary lateral veins, 2–8 mm from the margin, sunken above, raised below. INFLORESCENCE erect, longer than leaves; peduncle (30)70–130 cm long; spathe ovate-lanceolate, pale green, 8–13 cm long, 2.5–4.8 cm wide, acuminate at apex, rounded at base; spadix pale green, 5–12 cm long, ca. 9 mm diam. at base, ca. 6 mm diam. at apex; flowers sub-rhombic to 4-lobed, 2.2–2.5 mm long, 2.2–2.7 mm wide, the sides parallel to spirals usually straight, those perpendicular to spirals sigmoid; 8–9 flowers visible in the principal spiral, 12–18 flowers visible in the alternate spiral; tepals matte, minutely and densely papillate, lateral tepals 1.4–1.8 mm long, the inner margin straight; pistils weakly emergent, green; stigma brushlike and weakly exserted, glistening for 3 or 4 days before stamens emerge; stamens emerging in a scattered manner on fleshy, greenish, translucent filaments, lateral stamens emerged throughout before alternates appear, held at sides of pistil; anthers creamy white, 0.7–1 mm long, 1–1.2 mm wide; thecae ellipsoid, mounded with abundant, creamy white pollen. INFRUCTESCENCE not seen. Fig. 128.

Anthurium oerstedianum is endemic to Costa Rica at elevations of 900 to 1,300 m, principally from the Pacific slope in the southwest in premontane wet, tropical wet, and premontane rain forest.

Anthurium oerstedianum is distinguished by its strictly terrestrial habit as an understory forest herb and by its geniculum which is located 10–20 cm below the base of the blade. Other distinguishing features are its 4-sided petiole and its greenish spadix. The species is a member of section *Pachyneurium* despite its somewhat atypical elongate petioles, its remote geniculum, and lack of a densely rosulate habit.

Anthurium cuspidifolium, which is synonymous with *A. oerstedianum,* was reported by MacBride (1936) from Peru. However, the specimens cited by him [*MacBride 5622* (F); *Schunke 572* (F)] are referable to *A. flavescens* Poepp.

COSTA RICA. SAN JOSÉ: between San Isidro del General and Dominical, *Croat 35267* (MO); about one mile

FIGURES 124–127. 124–125. *Anthurium pallens* Schott, *Croat 48556.*—126. *Anthurium paludosum* Engl., *Kamemoto 309.*—127. *Anthurium panduriforme* Schott, *Croat 35587.*

FIGURES 128–131. 128. *Anthurium oerstedianum* Schott, *Croat 35293*.—129. *Anthurium ovandense* Matuda, *Croat 46164*.—130. *Anthurium panduriforme* Schott, *Las Cruces Bot. Gard. 74-513*.—131. *Anthurium parvispathum* Hemsl. (Cultivated at Birdsey's).

beyond divide between San Isidro del General and Dominical, *Croat 35293* (MO).

Anthurium ovandense Matuda, Anales Inst. Biol. Univ. Nac. México 30: 113–115, Fig. 7. 1960. TYPE: Mexico. Chiapas: Municipio Escuintla, Cerro Ovando (north of town of Escuintla) 1,400 m elev., *Matuda 32769* (MEXU, holotype). Note: Type description lists *Matuda 32768* as the type but the only specimen found at MEXU is numbered *32769*.

Anthurium ocotepecense Matuda, Anales Inst. Biol. Univ. Nac. México 27: 345, Fig. 4. 1957. TYPE: Mexico. Oaxaca: Cerro de Larion, Santo Tomás, Ocotepec, *MacDougall 321* (MEXU, holotype (?) not seen).

Epipetric or terrestrial to 1 m tall; stems 10–30 cm long, 2–3 cm diam.; leaf scars 2–2.7 cm wide; roots numerous, 5–6 mm diam., scurfy, brown; cataphylls green, 8–11 cm long, narrowly rounded at apex (acumen with subapical apiculum), drying tan, weathering at base into coarse fibers, remaining intact at apex. LEAVES erect-spreading; petioles terete, 29–75 cm long, 5–8 mm diam., weakly glaucous; geniculum 1.8–2 cm long, sometimes narrowly sulcate; blades narrowly-triangular, chartaceous, narrowly acuminate at apex, lobed at base, 18–53 cm long, 12–26 cm wide, broadest at base, the margins undulate to subcrispate; anterior lobe 14–38 cm long; posterior lobes 5.5–18 cm long; the sinus usually hippocrepiform, sometimes somewhat broader than deep; both surfaces matte to semiglossy with numerous linear raphide cells obscurely visible when fresh, clearly visible when dry; midrib weakly and convexly raised above and below, sunken at apex above; basal veins 4–5 pairs, the fourth and fifth coalesced 4–5.5 cm, raised above and below; primary lateral veins 5–10 per side, sunken above, raised below; interprimary veins sunken above, flat below; collective vein arising from the uppermost basal vein, 8–27 mm from margin. INFLORESCENCE erect to pendent; peduncle 32–72 cm long, 4–5 mm diam., terete; spathe green, subcoriaceous, lanceolate, 5–7.5 cm long, 1.5–2.4 cm wide, cuspidate-acuminate at apex, truncate to weakly clasping at base; stipe to 2.5 cm long in front, to 2.2 cm long in back; spadix green, 5–11 cm long, 6–9 mm diam.; flowers rhombic, 3–4 mm long, 2.5–3.5 mm wide, the sides straight to weakly sigmoid; 4–7 flowers visible in the principal spiral, 2–4 flowers visible in the alternate spiral; tepals glossy with abundant sticky droplets; pistils weakly raised; stigma linear, 0.5 mm long; stamens emerging rapidly from base, held in tight cluster over pistil; filaments white, translucent, retracting; anthers pale yellow; thecae ovoid, slightly divaricate; pollen pale yellow. INFRUCTESCENCE pendent; berries red, subglobose, usually developing only in lower one quarter of spadix. Fig. 129.

Anthurium ovandense is endemic to Mexico in southern Oaxaca and Chiapas in moist forest at elevations of 800 to 1,600 m.

The species is a member of section *Belolonchium* and is characterized by its usually epipetric habit, its thin narrowly ovate leaf blades with conspicuous posterior lobes, naked, gradually curved posterior rib, and an anterior lobe that is concave and generally undulate along the margins.

The species is similar to *A. umbrosum* from northern Oaxaca in generally much wetter areas and also to *A. lezamae* mostly from central Chiapas but both of these species are characterized by having their anterior lobe distinctly convex.

Matuda 37655, a sterile collection made at the type locality of *A. andresloviense* Matuda, was identified as that species by Matuda, but it is probably best placed with *A. ovandense.* It differs from typical *A. ovandense* in that the blade dries relatively more glossy on the upper surface and in having a distinct constriction at the base of the anterior lobe.

Although the type of *A. ocotepecense* was not seen, the illustration of the type appears to indicate that it is a synonym of *A. ovandense.* The type locality was not determined. Although I investigated part of the Municipio of Ocotepec and found it extremely arid, perhaps there may be other parts of the region that are more mesic. I was unable to locate a "Cerro de Larion" at Santo Tomás where the type was collected. The region where the type of *A. ocotepecense* was collected is substantially to the north of other collections.

MEXICO. CHIAPAS: Escuintla, Monte Ovando, *Matuda 32729* (MEXU). OAXACA: Cerro Concordia, *Morton & Makrinius 2727* (F, US); vicinity La Galera, *Croat 46164* (MO); Pluma Hidalgo, *MacDougall 715* (MEXU).

Anthurium pallens Schott, Oesterr. Bot. Z. 8: 180. 1858. TYPE: Costa Rica, near Desengaño, 2,600 m, *Wendland 840* (GOET).

Epiphyte, scandent; internodes 5–9 mm long;

cataphylls 4.5–5 cm long, drying reddish-brown, weathering into linear fibers and persisting. LEAVES erect-spreading; petioles subterete, 7–25 cm long, 2.5–6.5 cm diam., narrowly sulcate; blades lanceolate-linear to narrowly oblong-elliptic, 18–34.5 cm long, 2.5–6.5 cm wide, long-acuminate at apex, acute to obtuse or rounded at base; midrib raised above and below; primary lateral veins 5–9 per side, sunken above, raised below; lesser veins inconspicuous; collective vein arising from near the base. INFLORESCENCE ± erect, shorter than leaves; peduncle 10–16 cm long; spathe green, lanceolate, 2.5–3.2 cm long, 0.8–1 cm wide; spadix green turning yellow (sometimes orange), 3–4.5 cm long, 3–6 mm diam. (dry) at base, weakly tapered at apex; the flowers rhombic, ca. 3.1 mm long, 3 mm wide (dry); ca. 3 flowers visible in the principal spiral, ca. 5 flowers visible in the alternate spiral. INFRUCTESCENCE with spadix to 6 cm long; berries green to yellow-green (?), ± globose. Figs. 124 and 125.

Anthurium pallens is known from Costa Rica and Panama at 1,000 to 2,000 m elevation in premontane rain forest and lower montane rain forest life zones.

Anthurium pallens is easily confused with *A. microspadix* with which it shares similar habitats. It differs from *A. microspadix* by having blades acute to rounded at the base and clustered at the ends of relatively short branches with short internodes. It also has longer petioles and blades that dry characteristically gray-green and weakly glossy on the lower surface. *Anthurium microspadix* has long internodes with the leaves more widely and regularly spaced and blades that are rounded to subcordate at the base and generally matte on the lower surface upon drying. While both species may be epiphytic, *A. microspadix* generally is rooted in the soil and is an erect or semierect, vine-like plant, reclining or using trees for support. *Anthurium pallens* is usually a short-stemmed epiphyte that is frequently pendent.

Although mature berries have not been seen, they are no doubt yellowish-green and subglobose like those of *A. microspadix*. The species is a member of section *Xialophyllium*.

COSTA RICA. ALAJUELA: La Peña, *Smith 2121* (UC). HEREDIA: vicinity of Cerro Chompipe, *Wilbur & Luteyn 18584* (DUKE); Río Las Vueltas, *Burger & Liesner 6375* (MO); *Lellinger & White 988* (MO); *Lent 2638* (NY); *Wilbur & Luteyn 4414* (DUKE); *Taylor 17687* (NY); San Rafael, *Almeda et al. 2156* (DUKE, MO); *Wilbur et al. 15982* (DUKE); pass between Volcán Irazú and Volcán Barba, *Davidse & Pohl 1702A* (MO).

Anthurium paludosum Engl., Bot. Jahrb. Syst. 25: 401. 1898. TYPE: Colombia. Valle: near Buenaventura, *Lehmann 3811* (B, holotype).

Epiphyte; stems to 30 cm long; roots numerous, grayish-green, smooth, descending; cataphylls coriaceous, 5–6 cm long, persisting ± intact, drying brown, ultimately deciduous. LEAVES spreading-pendent; petioles 3–14 cm long, 3–5 mm diam., D-shaped to subterete, broadly and obtusely sulcate; geniculum 1–1.5 cm long; blades narrowly elliptic to oblanceolate, subcoriaceous, 10–38 cm long, 3–13.5 cm wide, short-acuminate at apex, acute to attenuate (rarely obtuse to subrounded) at base; both surfaces semiglossy, sparsely punctate; midrib convexly raised above and below, sunken at apex above; primary lateral veins 12–14 per side, departing midrib at 40° angle, sometimes weakly sunken, usually ± obscure on upper surface, prominulous on lower surface; collective vein arising from the base and extending ± straight to apex, 3–12 mm from margin, flat and nearly obscure on upper surface, prominulous on lower surface. INFLORESCENCE erect-spreading, shorter than leaves; peduncle 7.5–15.5 cm long, 3–5 mm diam., terete, tinged red-violet; spathe moderately thin, whitish to green or purplish, withering soon after anthesis, oblong-lanceolate, 5.5–7 cm long, 4–14 mm wide, acuminate at apex, rounded at base, inserted at ca. 60° angle on peduncle; spadix green, tinged orange, becoming violet-purple, 8–14.5 cm long, 6–7 mm diam. at middle, scarcely tapered at apex; flowers rhombic, 2.8–3.2 mm long, 2.5–2.7 mm wide, the sides straight or weakly sigmoid; 5–6 flowers visible in the principal spiral, 7–9 flowers visible per alternate spiral; tepals matte to semiglossy, tinged violet-purple at outer margins, lateral tepals 1.9–2 mm long, the inner margin broadly rounded; pistils green, weakly emergent; stigma linear; stamens emerging from base, the lateral stamens emerging with only the apex of the anther visible, retracting before alternate stamens emerge, leaving only traces of white pollen. INFRUCTESCENCE with spadix 6–25 cm long; berries orange, red-orange, or white tinged with orange, ± globose to ovoid, 4–6 mm diam.; seeds 3–4, ellipsoid-oblong; 2–2.5 mm long, yellowish, except green on one end. Fig. 126.

Anthurium paludosum is known from Costa Rica to Colombia at elevations from sea level to 400 m. It ranges along the Atlantic slope only west of the Isthmus of Panama. To the east of the Isthmus of Panama it occurs on both slopes until reaching South America, where it is restricted to the Pacific slope. The species occurs in wetter parts of tropical moist forest and premontane wet and tropical wet forest life zones.

Anthurium paludosum is a member of section *Porphyrochitonium* and is recognized by its coriaceous, almost oblong leaf blades that are more or less the same color on both sides with a pale green midrib on the upper surface, and by its thick, persistent, nondilacerating cataphylls and reddish-orange berries. No other species in this section is known to have cataphylls that remain intact.

In the revision of the Costa Rican *Anthurium* (Croat & Baker, 1979), *A. eggersii* Engl. was included as a synonym of this species, but examination of the type now precludes that possibility because that species has prominently dilacerating cataphylls. In other respects the two species appear to be markedly similar.

COSTA RICA. No other location, *Pittier 6837* (BR). LIMÓN: road between Bribrí & Bratsi, *Burger et al. 10470* (MO); between Limón & Puerto Viejo, *Baker & Burger 175* (MO).

Anthurium panduriforme Schott, Prod. Aroid. 536. 1860. TYPE: Costa Rica. San Miguel, *Wendland 776* (GOET).

Anthurium panduratum Schott, Oesterr. Bot. Z. 8: 182. 1858, non Mart. ex Schott, 1855. TYPE: Costa Rica. San Miguel, *Wendland 776* (GOET, holotype).

Epiphyte or occasionally terrestrial; stems usually less than 30 cm long, occasionally to 1 m long; roots numerous, scattered along stem; cataphylls moderately thin, 15–25 cm long, narrowly acuminate at apex, drying tan (B & K Yellow-red 9/10) usually deciduous, with a few thin fibers sometimes persisting. LEAVES moderately thin; petioles 25–73 cm long, 3–7 mm diam., terete, sometimes weakly sulcate; geniculum 1.5–2 cm long; blades hastate-trilobate, erect or spreading from the erect petioles, 20–65 cm long, 10–43 cm wide, gradually to abruptly acuminate at apex, prominently lobed at base; anterior lobe 21–55 cm long, constricted near base; posterior lobes nearly orbicular (or rarely oblong), sometimes directed conspicuously upward from point of petiole attachment; sinus usually spathulate or hippocrepiform sometimes parabolic, usually rounded at apex; both surfaces semiglossy to glossy; midrib obtusely raised above, sunken toward apex, prominently raised below; primary lateral veins 15–30 per side, departing midrib at 45°–50° angle, sunken above, raised below; lesser veins less conspicuous; basal veins 5–9 pairs, 3–4 coalesced 1–4.5 cm; posterior rib naked, weakly turned up along outer margin; collective vein arising from one of the lowermost basal veins and extending to apex, 3–7 mm from the margin. INFLORESCENCE erect, shorter than leaves; peduncle (5)11–20(32) cm long, 4–6 mm diam., terete; spathe moderately thin, pale green, sometimes tinged reddish, oblong-lanceolate, 6.3–19 cm long, 2.7–3.5 cm wide, abruptly acuminate at apex, rounded at base, inserted at 60° angle on peduncle; spadix golden yellow (B & K Yellow-red 8/10), 7–18 cm long, 7–9 mm diam. midway, tapered to 4–6 mm at apex; the flowers sub-4-lobed, 2.5–3 mm long, 2.9–3.3 mm wide, the sides ± straight to jaggedly sigmoid; 6–9 flowers visible in the principal spiral, 6–10 flowers visible in the alternate spiral; tepals yellow, glossy, lateral tepals 1–1.5 mm wide, the inner margin convex; pistils weakly emergent, pale green, translucent; stigma linear, ca. 0.3 mm long, brushlike and glistening as anthers emerge; stamens emerging in scattered manner slowly from base to apex, exserted to ca. 1.3 mm on white or translucent, flat filaments, the exserted portion of the filaments ca. 0.3 mm long, ca. 0.5 mm wide; anthers yellow, 0.5–0.6 mm long, 0.7–0.9 mm wide; thecae divaricate; pollen golden yellow. INFRUCTESCENCE arching-pendent; the spadix to 23 cm long; berries pale green, ovoid, 5–7 mm long; seeds 2, greenish-white, 2.6–3 mm long, 2.3–2.5 mm wide, 0.8–1 mm thick. Figs. 127 and 130.

The species is known from Costa Rica to Colombia and probably Ecuador at 400 to 1,560 m elevation in tropical wet, premontane rain, and lower montane rain forest. In Costa Rica, the species ranges from Bijagua in the north to Tapantí in the south on the Atlantic slope. In Panama the species occurs on both slopes.

Anthurium panduriforme is distinguished by its almost orbicular posterior lobes (sometimes more elongate in Panama, particularly collections made at Cerro Tute, near Santa Fe, Vera-

guas), its characteristically yellow-green, shiny lower blade surface, and its golden yellow spadix with yellow pollen. The species is apparently not related to any other Central American species. It is probably best placed in section *Polyneurium* and is no doubt related to other South American species such as *A. argyrostachyum* Sodiro of Ecuador that have numerous closely parallel primary lateral veins.

COSTA RICA. San Miguel, *Wendland 776* (GOET). ALAJUELA: NNE of Bijagua, *Croat 36286* (MO); N of Coliblanco, *Utley & Utley 4687* (DUKE, MO); between Naranjo & Aguas Zarcas, *Croat 46974* (MO); N of San Ramón, *Luteyn 3372* (DUKE); N of La Balsa de San Ramón, *Utley & Utley 4583* (DUKE); valley of Río Sarapiquí, between Vara Blanca & Cariblanco, *Moore 6614* (BH). HEREDIA: vicinity Bajo La Hondura, *Croat 44515* (MO); N of Vara Blanca, *Croat 35587* (MO). LIMÓN: vicinity Guapiles, *Standley 37255* (US).

Anthurium parvispathum Hemsl., Biol. Cent. Amer., Bot. 3: 432. 1885. TYPE: Guatemala. Baja Verapaz: Santa Rosa, *Salvin & Godman 408* (K, holotype).

Anthurium hypoleucum Standl., J. Wash. Acad. Sci. 17: 246. 1927. *Anthurium brevipetiolatum* Engl. ex K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11: 610. 1932. TYPE: Guatemala. Baja Verapaz: Santa Rosa, 1,600 m, *Tuerckheim II.2214* (US-932125, holotype; B, isotype).

Epipetric; stem short; roots thick, tan, sometimes directed upward; cataphylls ca. 7 cm long, drying brown, persistent, weathering to coarse linear fibers. LEAVES spreading; petioles 16–50 cm long, 6–9 mm diam., broadly and sharply sulcate, weakly glaucous; geniculum 1.3–1.5 cm long; blades oblong to lanceolate, subcoriaceous, acute at apex, truncate at base, 27–64 cm long, 6.5–12 cm wide; both surfaces matte and glaucous, the lower surface only slightly paler; midrib convexly raised above, diminished and sunken at apex, more acutely raised below; basal veins one pair, sunken above, raised below; primary lateral veins 6–10 per side, departing midrib at 40° angle, sunken above, raised below; interprimary veins weakly sunken above, flat below; lesser veins obscure; collective vein arising from the basal vein, 8–10 mm from margin, sunken above, raised below. INFLORESCENCE spreading, shorter to as long as leaves; peduncle 31–52 cm long, subterete, 1–2 faint ribs; spathe subcoriaceous, green (B & K Green 5/7.5), lanceolate, 3.5–7 cm long, 1–2 cm wide, long-acuminate at apex, clasping at base, inserted at 180° angle on peduncle; spadix sessile, green (B & K Yellow-green 7/7.5) becoming pale yellow, 3.5–9 cm long, 7–10 mm diam. at base, 3–5 mm diam. at apex; flowers 4-lobed, ca. 2.3 mm in both directions, the sides jaggedly sigmoid; 5–7 flowers visible in the principal spiral, 7–9 flowers visible in the alternate spiral; tepals matte, lateral tepals ca. 1 mm wide, the inner margin convex; pistils green, weakly emergent; stigma slit-like; stamens emerging from the base, laterals emerging first, followed quickly by alternates, the leading stamen preceding fourth stamen by 1–3 spirals. INFRUCTESCENCE pendent, mature berries not seen. Fig. 131.

Anthurium parvispathum is endemic to Guatemala and is known principally from Baja Verapaz at 1,500 to 1,800 m elevation, but it is also known from single collections from the Sierra de la Minas in Zacapa Department and at Mazatenango in the Dept. of Suchitepéquez on the Pacific Coast. The species occurs principally in open or exposed areas on rocks in areas of dry forest.

The species is a member of section *Belolonchium* and is characterized by having a sessile spadix and oblong-lanceolate leaves that are at least initially glaucous (often drying whitish) on the lower surface and by having the primary lateral veins equally as prominent as the basal vein. The species is also characterized by occurring on rocks.

Anthurium parvispathum is similar to *A. nakamurae* from southeast Chiapas but differs in having thicker leaves, which are generally much paler and weakly glaucous on the lower surface. In addition, it is always found growing on rocks rather than as an epiphyte. The spadix of *A. parvispathum* is always sessile whereas that of *A. nakamurae* is stipitate at least to some extent.

Anthurium parvispathum has also been confused with *A. retiferum*, which has a similar leaf shape and venation, but that species has much broader leaves that have conspicuously elevated tertiary veins on drying and is not glaucous or pale on the lower surface. It has also been confused with some leaf forms of *A. subcordatum* but that species differs in having the basal veins much more conspicuous than the primary lateral veins.

GUATEMALA. BAJA VERAPAZ: N of Salamá, near Pantín, *Williams et al. 42194* (F, NY); above Pantín, *Williams et al. 43354* (F); Santa Rosa, *Standley 6969*[illegible] *91242, 91258, 91271* (F); *Tuerckheim 2214* (US). SUCHITEPÉQUEZ: Mazatenango, *Tejada 306* (US). ZACAPA: Río Nuevo Sitio, between Santa Rosalía & Is[illegible] waterfalls, *Steyermark 42212* (NY).

Anthurium pedatoradiatum Schott, Bonplandia 7: 337. 1859.

a. **Anthurium pedatoradiatum** ssp. **pedatoradiatum.** TYPE: Mexico, cultivated in Vienna, illustrated by Schott Aroid Drawing #781, 782, NYBG Neg. #3920, 3921; Photo MO.

Anthurium pedatifidum Regel & Linden, Gartenflora 15: 66. 1866. TYPE: Plate 501 accompanying the description (see discussion).

Anthurium mirandae Matuda, Anales Inst. Biol. Univ. Nac. México 22: 375. 1951. TYPE: Mexico. Chiapas: El Ocote, NW of Ocozocoautla, elev. 575 m, *Miranda 6312* (MEXU).

Terrestrial, usually more than 1 m tall; stem 1.7–3 cm diam.; leaf scars 2 cm wide; roots moderately thick, directed downward; cataphylls subcoriaceous, 3.5–4 cm long, rounded at apex, drying medium brown (B & K Yellow 5/5), persisting intact at apex, splitting at base. LEAVES erect; petioles 35–87 cm long, 5–6 mm diam., terete; geniculum 1–1.2 cm long; blades broadly ovate, 22–33 cm long, 38–60 cm wide, broadest at middle or just below, to 13-pedatisect, the lobes confluent 4–7 cm from base, the base broadly lobed, the apices of the lobes narrowly acuminate, the margin of the lobes entire, the median lobe 18–33 cm long, the outermost lobes 18–27 cm long, inequilateral and auriculate, falcate; sinus hippocrepiform, rounded at apex; upper surface semiglossy, the lower surface matte; midrib of the median lobe sharply raised above and below; basal veins 3–5 pairs, the third to fifth coalesced 1.5–1.8 cm, the fourth to fifth coalesced to 5.5 cm, raised above and below; primary lateral veins of the median lobe 4–8 per side, departing the midrib at ca. 40° angle, sunken above, raised below, loop-connecting; collective vein of the median lobe arising from the first or second primary lateral vein. INFLORESCENCE erect, shorter than leaves; peduncle 5–23 cm long, 3 mm diam.; spathe green (B & K Yellow-green 7/7.5), lanceolate, 7–9.2 cm long, 1.5 cm wide, inserted at 50° angle on peduncle; stipe 18 mm long in back; spadix greenish tinged with purple-violet to dark purple-violet (B & K Red-purple 2/10), 4–7.5 cm long, 5–7 mm diam. at base, 3–4 mm diam. at apex; flowers rhombic to sub-4-lobed, 4–4.8 mm long, 4.2–4.4 mm wide, the sides sigmoid; 6–7 flowers visible in the principal spiral, 4–5 flowers visible in the alternate spiral; tepals matte, minutely papillate, the lateral tepals 2.4–2.5 mm wide, the inner margins broadly rounded; pistil raised but not emergent; stigmas obscure; stamens emerging in a slow progression from base, the alternate stamens following soon after emergence of both lateral stamens, exserted above the tepals and held in a tight circle over pistil; filaments whitish, translucent 0.5 mm long, 0.1 mm wide, flattened; anthers white to pale yellow, 0.5–0.6 mm long, 0.5–0.6 mm wide; thecae narrowly ovate, slightly divaricate; pollen pale yellow to cream, fading to white. INFRUCTESCENCE unknown. Figs. 134 and 141.

Anthurium pedatoradiatum consists of two subspecies, both endemic to Mexico. The species occurs in southern Veracruz, Chiapas, and Tabasco ranging in elevation from near sea level to 800 m. Most collections have been made above 500 m in a region of "selva alta perennifolia" north of Ocozocoautla, a region with extensive outcrops of limestone.

The species is in section *Schizoplacium* and is distinguished by the pedatisect leaf blades with entire lobes, erect inflorescences that are shorter than the leaves, and the green, lanceolate spathe.

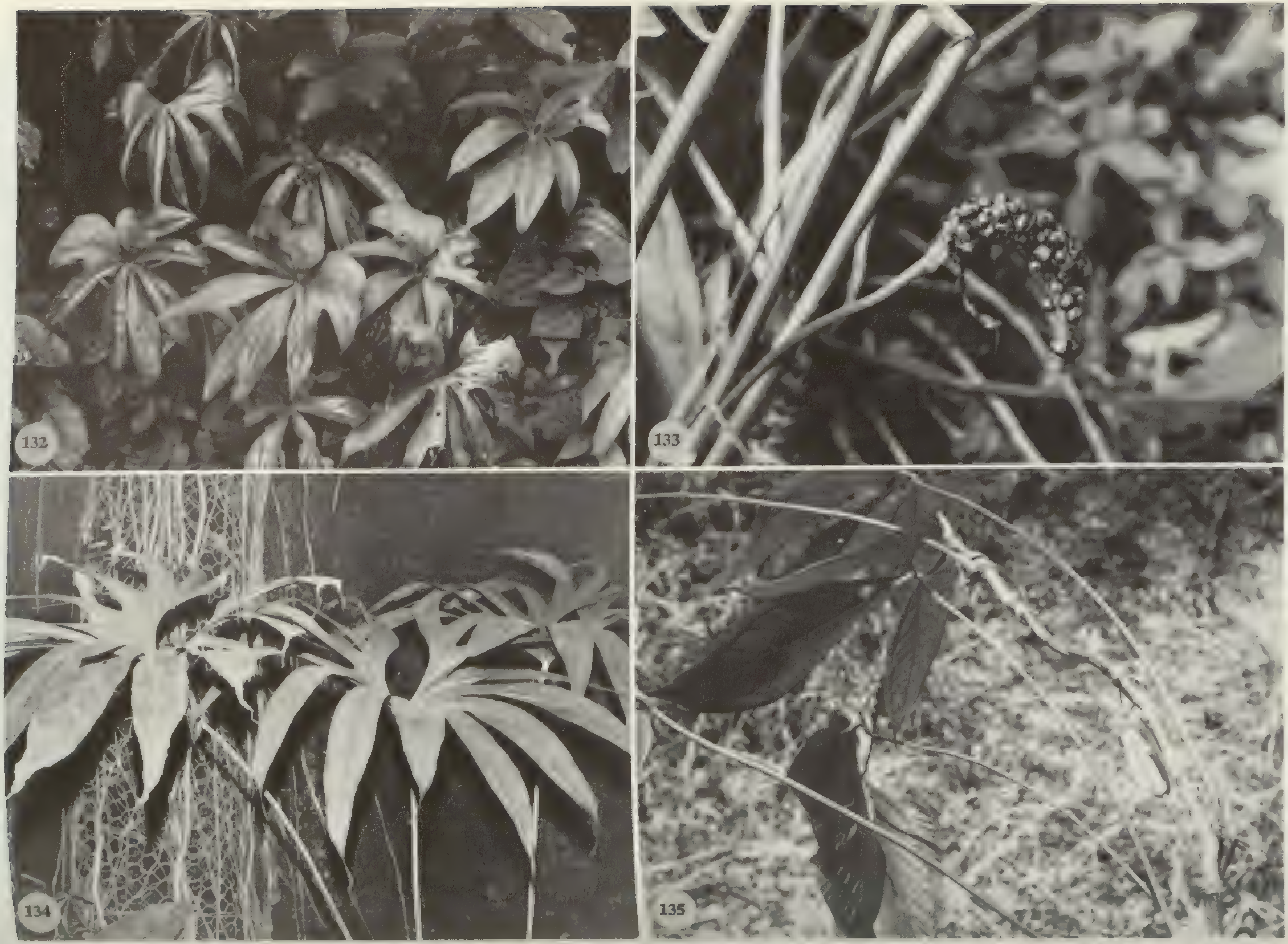
In Mexico it is possible to confuse the species with some forms of *A. podophyllum,* which may have the leaf segments entire. The latter occur only in northern Oaxaca and can be distinguished by having much thicker leaf blades.

The subspecies *pedatoradiatum* is distinguished by its terrestrial habit and differs from subspecies *helleborifolium* by having leaf segments rather uniformly united at the base with no segments divided to the base of the leaflet. In subspecies *helleborifolium,* one or more of the segments is free or nearly free to the base.

The plate accompanying the type description of *A. pedatifidum* shows a plant with one leaf blade divided in the manner characteristic of subspecies *pedatoradiatum* and another seemingly divided to the base, but nothing is mentioned in the description about this range of variation and it can only be assumed that the second leaf represents an error by the artist. The taxon that is here considered a synonym was supposed to differ from *A. pedatoradiatum* by a supposedly different geniculum and fewer number of blade segments.

MEXICO. CHIAPAS: N of Ocozocoautla, *Breedlove 38250* (DS); *Croat 40654* (MO); *Kennedy 1482* (DUKE, MO); *MacDougall s.n.* (MEXU); *Miranda 6312, 25931* (MEXU); *Ton 3800* (DS, LL). OAXACA: Río de la Venta, *MacDougall s.n.* (MEXU). TABASCO: Munc. Huimanguillo, *Gilly & Hernandez 103* (MICH).

b. **Anthurium pedatoradiatum** ssp. **helleborifolium** (Schott) Croat, comb. nov. *Anthurium*



FIGURES 132–135. 132–133. *Anthurium pedatoradiatum* ssp. *helleborifolium* (Schott) Croat, *Croat 40081*. — 134. *Anthurium pedatoradiatum* Schott, Kew 504-69-04135. — 135. *Anthurium pentaphyllum* var. *bombacifolium* (Schott) Madison, *Croat 32910*.

FIGURES 136–139. 136. *Anthurium pittieri* Engl., *Kamemoto 260.*—137. *Anthurium pittieri* Engl., *Croat 35981.*—138. *Anthurium pittieri* var. *fogdenii* Croat, *Croat 47134.*—139. *Anthurium pittieri* var. *fogdenii* Croat, *Croat 46771.*

FIGURES 140–143. 140. *Anthurium pedatoradiatum* ssp. *helleborifolium* (Schott) Croat, *Croat 40081.*—141. *Anthurium pedatoradiatum* Schott, (*Hort. Paris, Croat Neg. #500*).—142. *Anthurium pentaphyllum* var. *bombacifolium* (Schott) Madison, *Folsom s.n.*—143. *Anthurium pluricostatum* Croat & Baker, *Croat 43206.*

helliborifolium Schott, Bonplandia 10: 148. 1862. TYPE: Mexico. No specimen cited in original description (F, hololectotype, FM 29818; Photo of cultivated plant prepared by Schott here designated).

Terrestrial; ca. 1 m or less tall; stems thick, 9–25 cm long, 2–3 cm diam.; internodes very short; leaf scars 2 cm wide, usually obscured by cataphylls; roots medium thick, descending; cataphylls subcoriaceous, 2.5–5.3 cm long, sometimes tinged reddish, drying medium brown (B & K Yellow 5/5), splitting at base, remaining intact at apex, persisting around stem. LEAVES with petioles erect, (27)48–56(63) cm long, 8–9 mm diam., terete; geniculum 1–1.7 cm long; blades, 7–11 pedatisect, moderately thick, broadly ovate in outline, deeply lobed at base, 27–33.5 cm long, 18–48 cm wide, broadest at middle or just below; the lobes free or nearly so to base, the outermost lobes confluent to a greater degree, sometimes falcate, acuminate at apex, the median lobe 21–27 cm long, 5.7–7.9 cm wide, broadest just above middle, outermost lobes 12–18 cm long, markedly inequilateral and usually auriculate; sinus narrowly to broadly spathulate to hippocrepiform, acute to rounded at apex; the upper surface glossy, lower surface semiglossy; the midrib of the median lobe acutely raised above, diminished and sunken at apex, raised below; primary lateral veins 3–4, departing midrib at 40°–50° angle, sunken and nearly obscure above, raised below; basal veins 5–6 pairs, the first and second free to base, the remaining coalesced 1.5–4 cm, raised above and below; the posterior ribs weakly curved, naked ca. one half their length; collective vein arising near the base of lobe, or from one of the primary lateral veins near middle, 1–5 mm from margin. INFLORESCENCE erect, shorter than leaves; peduncle (8)20–30 cm long, 3–5 mm diam., terete; spathe moderately thin, green, lanceolate, 5.5–11 cm long, 0.6–1.5 cm wide, gradually acuminate at apex, rounded at base, inserted at ca. 45° angle on peduncle; spadix green (B & K Yellow-green 5/7.5), 4–8 cm long, 4–6 mm diam. at base, 2–3 mm diam. at apex; the flowers rhombic to sub-4-lobed, 2.5–3 mm long, 2.8–3.2 mm wide, the sides smoothly sigmoid; 3–5 flowers visible in the principal spiral, 4–6 flowers visible in the alternate spiral; tepals matte, densely papillate, lateral tepals 1–1.5 mm wide, the inner margin straight; pistils emergent, only slightly raised, green, densely papillate; stigma linear, 4–5 mm long, dark slit with red-violet punctations; stamens emerging from the base, lateral stamens preceding alternates by 1–2 spirals, exserted on long, translucent filaments, 0.5–0.8 mm long, 0.9–1 mm wide, retracting to hold stamens at edge of pistil; anthers yellow to tan, sometimes deep purple; thecae ellipsoid, somewhat divariate; pollen cream to yellow. INFRUCTESCENCE not seen. Figs. 132, 133, and 140.

Anthurium pedatoradiatum ssp. *helleborifolium* is endemic to southern Mexico in Chiapas and Tabasco where it is common in "selva alta perennifolia" in the vicinity of Teapa, Tabasco. All collections seen were made at elevations of less than 300 m. Plants are terrestrial, commonly well rooted in the soil but generally on well drained soil, usually over porous limestone, commonly on rocky slopes.

Anthurium pedatoradiatum ssp. *helleborifolium* differs from ssp. *pedatoradiatum* in having 1–3 of the medial blade segments free or nearly free to the base. In addition, those collections of ssp. *helleborifolium* grown side by side in the greenhouses with ssp. *pedatoradiatum* have consistently darker green, thicker leaves. Madison (1978) treated ssp. *helleborifolium* as synonymous with *A. pedatoradiatum* but I feel they are separable at least at the subspecific level. All of the material observed thus far has been easily separable on the key characters although some specimens with a poor state of preservation appeared to have free segments because of torn segments. A collection of *Bunting and Davies* (*117*) collected near Teapa was deemed intermediate by Bunting (1965) who reported that it differed in "having the outline of the former but with the central lobe free to the very base." I have found that the outline of the leaf blades of the species are very generally the same and the division of the leaf blade of the Bunting and Davies specimen is well within the range of variation for the species.

Since no type specimen was cited I have selected as a lectotype a collection prepared and annotated by H. C. Schott from a cultivated plant in Vienna. Although the specimen itself has been destroyed, the photographs of the specimen are widely distributed as Field Museum plate #29818.

MEXICO. CHIAPAS: between Ixtapa and Teapa, *Croat 47899* (MO); vicinity Pichucalco, *Croat 40081* (MO).

TABASCO: N of Cerro de Azufre, *Gilly & Hernandez 296* (MEXU, MICH); base of Cerro de Madrugal, *Croat 47906* (MO); Tacotalpa, *Cowan 2062* (MO); E of Teapa, *Croat 40130* (MO); *Conrad & Gallegos 2869* (MO).

Anthurium pentaphyllum (Aubl.) G. Don in Sweet, Hortus Brit. ed. 3: 633. 1839.

Anthurium pentaphyllum var. **bombacifolium** (Schott) Madison, Selbyana 2: 278. 1978. *Anthurium bombacifolium* Schott, Oesterr. Bot. Z. 8: 182. 1858. TYPE: Costa Rica. Near Atenas, *Hoffmann 779* (B, destroyed; Photo of Schott Aroid Drawing #829, NYBG Neg. #N.S. 3934).

Anthurium aemulum Schott, Bonplandia 7: 165. 1859. TYPE: Mexico. Colipa, *Liebmann 15799* (C?, not seen).

Anthurium karwinskyi Schott, Oesterr. Bot. Z. 9: 101. 1859. TYPE: Mexico. Veracruz: Colipa, *Karwinsky* (LE).

Epiphyte; stems creeping up tree trunks; internodes 2–9 cm long; cataphylls caducous or persisting as coarse fibers. LEAVES erect-spreading; petioles 19–44 cm long, ca. 5 mm diam., terete; blades digitately compound with 5–11 leaflets, moderately thin, leaflets oblanceolate to narrowly elliptic, 13–30 cm long, 2.5–9 cm wide, the medial leaflet equilateral, the lateral leaflets inequilateral, abruptly to cuspidate-acuminate at apex, cuneate-attenuate at base; midrib raised above and below; primary lateral veins 6–8 per side in each leaflet, sunken above, raised below; lesser veins obscure above, raised below; collective vein arising from base, 6–14 mm from margins, ± straight to apex of leaflet. INFLORESCENCE erect; peduncle 1–6 cm long; spathe pale green to purple, lanceolate to ovate, moderately thick, 6–10 cm long, 1–2.8 cm wide, early deciduous; spadix pale purple-violet, 2.2–10(15) cm long, 8–20 mm diam. at base, tapering at apex. INFRUCTESCENCE erect-spreading; berries red to dark red-violet, ± globose, 5–8 mm diam.; seeds ovoid to oblong, ca. 5.3 mm long and 4 mm wide. Figs. 135 and 142.

Anthurium pentaphyllum var. *bombacifolium* is known from Mexico to Panama at elevations from near sea level to 800 m, occurring principally on the Atlantic slope in Mexico and Middle America but on both slopes in Costa Rica and Panama. The species occurs in premontane moist, tropical moist, premontane wet, and tropical wet forest life zones, making it one of the most ecologically variable species of *Anthurium* in Central America.

The species is a member of section *Dactylophyllium* and is most easily confused with *A. kunthii,* which has similar leaves, but *A. kunthii* differs in having a longer peduncle, three-quarters the length of the petiole, and in having a long, slender, greenish spadix and lateral leaflets which are more or less equilateral at the base.

BELIZE. BELIZE: Gracy Rock, Sibun River, *Gentle 1741, 1744* (MICH); *Gentle 1491* (MICH, MO). CAYO DISTRICT: near Camp 6, *Gentle 2417* (MICH); Caves Branch, Base of Mountain Cow, *Whitefoord 1082* (MO); Cuevas, Little John's Hunting Camp, *Dwyer 11560* (MO); Macaw River, road to Millionario, *Dwyer & Liesner 12343* (MO); Mountain Cow Ridge, *Gentle 3553, 3526* (MICH); Vaca, *Gentle 2551* (MICH); Valentin Camp, *Lundell 6197* (MICH). STANN CREEK DISTRICT: Big Creek, *Gentle 2651* (MICH); S of Lyman Agricultural School, *Spellman 1604* (MO); Middlesex, *Gentle 2950* (MICH); Stann Creek Railroad, *Gentle 2109* (MICH); near Railway, *Schipp S-279* (MICH, MO, UC); N of Victoria Peak, *Gentry 8025* (MO). TOLEDO: W of Columbia Forest Station, *Croat 24300* (MO); *Dwyer 9859* (MO); Punta Gorda, *Cosminsky 224* (F); Río Grande, *Gentle 4679* (LL, MICH); near San Antonio, *Gentle 6648* (LL); Swasey Branch, Monkey River, *Gentle 3955, 4010* (MICH).

COSTA RICA. ALAJUELA: vicinity Bijagua, *Croat 36265, 36424* (MO); Fortuna, *Taylor 11615* (NY); beyond San Ramón, *Luteyn 3384A* (DUKE); NW of Zarcero, *Croat 43585* (MO). HEREDIA: Puerto Viejo, *Croat 35684* (MO). LIMÓN: between Limón & Shirores, *Croat 43297* (MO); between Siguerres and Río Pacuare, *Burger & Liesner 6948* (MEXU, MO). PUNTARENAS: Corcovado National Park, *Liesner 2831* (MO); above Palmar Norte, *Croat 35124* (MO); between Palmar Sur and Piedras Blancas, *Croat 32910* (MO); S of Puerto Armuelles, *Liesner 181* (MO).

GUATEMALA. ALTA VERAPAZ: Finca Argentina above Papalhú, *Croat 41565* (MO); road to Oxec, between Tucurú and El Estor, *Croat 41685* (MO). IZABAL: vicinity of Puerto Barrios, *Croat 41824A* (MO). PETÉN: no other location, *Lundell 2990* (MICH); Cerro Ceibal, *Steyermark 46104* (LL); vicinity Archeological camp, N shore of Lake Yaxja, *Croat 24677* (MO); La Libertad, *Lundell 3054* (MICH); Tikal, *Bartlett 12581* (MICH); Uaxactún, *Bartlett 12466* (MICH); *Bartlett 12269* (MICH, UC).

HONDURAS. ATLÁNTIDA: vicinity La Ceiba, *Yuncker et al. 8597* (MO); Lancetilla, *Chickering 134* (MICH); *Croat 42637* (MO); *Yuncker 4932* (MICH). COPÁN: S of Nueva Arcadia, *Harmon & Fuentes 6421* (UMO).

MEXICO: CHIAPAS: Municipio of Berriozábal, *Breedlove 26341* (DS); N of El Truinfo, *Almeda 3427A* (DUKE); NE of Escuintla, *Croat 43824* (MO); *Matuda 980* (MEXU, MO); *Matuda 16566* (DS, MEXU); *Matuda 17793* (DS, MEXU, UCLA); *Matuda 17794* (DUKE, MEXU); *Matuda 18720* (MEXU); *Matuda 37678* (DS); Islamapa, Huehuetán, *Matuda 18021* (MEXU); Nandolopez, Acapetagua, *Matuda 17867* (MEXU); Municipio Ocosingo, *Breedlove 34003, 34496* (DS); N of Ocozocoautla, *Croat 40637* (MO); Municipio of Palenque, *Breedlove 26543, 34997* (DS); *Croat 40235, 40268, 40339* (MO); vicinity of Pichucalco, *Croat 40072, 40148* (MO); N of Tapachula, *Croat*

43793 (MO); NW of Turquiz, *Croat 47476* (MO); E of Zapata, *Davidse & Davidse 9432* (MO); OAXACA: Chiltepec, *Sousa 1726* (MEXU); between Palomares and Río del Corte, *MacDougall s.n.* (MEXU); Temascal, *Sousa 1826* (MEXU); S of Valle Nacional, *Croat 39719* (MO); NE of Valle Nacional, *Moore & Bunting 8916* (BH). SAN LUIS POTOSÍ: vicinity Tamazunchale, *Croat 39274* (MO); *Rzedowski 10992* (CAS, MICH). TABASCO: along Río Chinal above Mascupan, *Gilly & Hernandez 383* (MEXU, MICH). VERACRUZ: Coatzacoalcos, *Williams 8721* (MICH); vicinity of Martínez de La Torre and Misantla, *Gomez-Pompa & Riba 201* (MEXU); *Moore & Bunting 8948* (BH); Tuxpan, *Sarukhán & Martinez s.n.* (MEXU). PUEBLA: La Granja, *Sarukhán & Martinez s.n.* (MEXU).

NICARAGUA. ZELAYA: Caño Costa Riquita, *Stevens 5057* (MO); S of bridge at Colonia Agrícola Yolaina, *Stevens 4820, 6353* (MO); W of Río Wawa Ferry, *Stevens 8646* (MO); near Río Yaoya, *Neill 3801* (MO); SW of Waspán, *Atwood 3716* (MO).

Anthurium pittieri Engl., Bot. Jahrb. Syst. 25: 372. 1898.

a. **Anthurium pittieri.** var. **pittieri.** TYPE: Costa Rica. Heredia: Rancho Flores, Volcán Barba, 2,505 m, *Pittier & Durand 865* (BR, hololectotype, designated Croat & Baker, 1979).

Epiphyte, sometimes somewhat scandent; stems less than 30 cm long; internodes short, 1–1.5 cm diam., leaf scars conspicuous; roots few, descending; cataphylls subcoriaceous, (3)8–12.5(14) cm long, apiculate at apex, drying dark tan, persisting intact, ultimately deciduous. LEAVES spreading; petioles 3–15 cm long, 4–7 mm diam., subterete, usually bluntly sulcate to weakly flattened; geniculum 2–3 cm long; blades narrowly lanceolate to lanceolate-elliptic to ovate-elliptic or oblong, moderately thick, (8.5)10–43 cm long, 1.5–9 cm wide, acuminate at apex, acute to obtuse or rarely rounded at base; upper surface matte to semiglossy, lower surface semiglossy; midrib broad and convexly raised above and below, diminished and sunken at apex above; primary lateral veins 17–20 per side, ± obscure above, prominulous to flat and ± obscure below, departing midrib at ca. 50° angle, straight to collective vein; collective vein arising near the base, weakly sunken above and prominulous below, 3–6 mm from margin. INFLORESCENCE ± erect, usually shorter than leaves; peduncle (5)11–14 cm long; spathe green, subcoriaceous, oblong-lanceolate, (3)7–15 cm long, 1.2–2.5 cm wide, caudate-acuminate at apex, decurrent onto peduncle 1–1.5 cm, acute to attenuate at base, inserted at 80° angle on peduncle; spadix green (B & K Yellow-green 5/7.5), (2.2)11–14.5 cm long, (3)7–8 mm diam. at base, (2)4–5 mm diam. at apex; flowers rhombic, 6–6.3 mm in both directions, the sides straight to weakly sigmoid; 2–3 flowers visible in the principal spiral, 3–5 flowers visible in the alternate spiral; tepals matte, minutely papillate, larger plants with tepals usually mounded giving spadix a knobby appearance, lateral tepals ca. 5 mm wide, the inner margin straight; pistils usually exserted, green, matte; stigma elliptic, ca. 0.6 mm long, brushlike, exserted and glistening with a small droplet for 3 or 4 days ca. 2–3 weeks before anthers emerge, dry and black as stamens emerge; stamens emerging slowly in scattered manner throughout spadix, exserted on minute, green filaments that retract holding anthers at sides of pistil; anthers cream-colored ca. 0.5 mm long, ca. 1 mm wide; thecae tan, ellipsoid, not divaricate; pollen pale yellow fading to white, soon dispersing. INFRUCTESCENCE pendent; spadix 5–15 cm long; berries yellow to orange in Panama or reportedly white in Costa Rica, obovoid, acute at apex, 1–1.5 cm long, 7 mm wide; seeds 2, green, flattened. Figs. 136 and 137.

The species is known from Costa Rica and Panama at 50 to 2,100 m elevation in tropical wet and premontane rain forest life zones. A specimen recently collected by Ernesto Ancuash (*1230*) under the auspices of Brent Berlin's anthropological studies in Peru (Dept. of Amazonas, Río Cenepa) is apparently also this species. It would be the first collection of the species from South America.

Anthurium pittieri is a member of section *Oxycarpium* and is distinguished by its coriaceous, epunctate leaf blades, premature emergent berries, and especially by the long-decurrent spathe.

The species is variable in leaf blade shape and in the degree of emergence of the pistils. Smaller plants tend to have the tepals flat with the pistils not noticeably emergent while larger plants have the pistils somewhat protrudent with the tepals turned somewhat upward. Specimens with unusual leaf shape include *Antonio 2139* from Panama with oblong leaves, 6.5 times longer than wide and *Croat 35295* from Dominical (Puntarenas, Costa Rica) with leaves almost as wide as long.

It is most easily confused with *A. interruptum* and *A. carnosum*, both of which differ in usually having more elongate internodes, in lacking a conspicuously decurrent spathe, and in having either green or reddish berries. *Anthurium pittieri* is reportedly related to *A. decurrens* Poepp. from

Amazonian Peru but differs from that species in having a much shorter stipe.

Costa Rica. No other location, *Bogner 917* (M). alajuela and puntarenas: Monteverde, *Utley & Utley 2396* (MO); *Burger & Baker 9645* (MO); *8750* (F). alajuela: Hacienda Santa Elena, *Austin Smith 1511* (NY); Santa Rosa National Park, *Liesner 5215* (MO); road from Sucré towards Lake Pozo Verde, *Luteyn et al. 4500* (DUKE); region Zarcero, *Austin Smith 114, 293* (MO). cartago: no other location, *Madison 6968* (MO); La Carpintera, *Allen 512* (MO); *Brade 2514* (BR); *Rodrigues 496* (UC); El Muñeco, *Standley & Torres 51671* (US); between Moravia & Quebrada Platanillo, *Croat 36646* (MO); vicinity Orosi, *Standley 39903* (US); S of Tapantí, *Burger & Liesner 6724A* (MO); *Lent 904* (CAS); SE of Turrialba, *Holm & Iltis 194* (NY). guanacaste: Hacienda Santa María, *Dodge et al. 6366* (MO); Monteverde, *Primack et al. 436* (DUKE). heredia and san josé: Slopes of Cerro Zurquí, *Luteyn & Wilbur 4468* (DUKE, MO). heredia: Las Lajas, vicinity San Isidro, *Pittier 14057* (NY); N of San Isidro, Cerro de Las Lajas, *Standley & Valerio 51634, 51564* (US); Monte Cristo, *Rojas s.n.* (MO); Rancho Flores, *Pittier & Durand 865* (BR); *Pittier 2157* (BR); Río Las Vueltas, *Gomez 2228* (MO); Vara Blanca, *Skutch 3650* (MICH); *3687* (MICH, MO, NY); *3694* (MICH, NY, US); *3704* (MICH); *Utley & Utley 4978* (DUKE); slopes of Volcán Barba, *Almeda 519* (DUKE); *Burger & Stolze 6068* (NY). puntarenas: Monteverde, *Utley 150* (DUKE); S of San Vito de Java, *Raven 21927* (CAS). san josé: slopes of Cerro Zurquí, *Utley 404* (DUKE); La Palma, *Luteyn 3303* (DUKE); between San Isidro del General & Dominical, *Croat 35925* (MO); San Josecito, *Primack & Luteyn 352* (DUKE); Tablazo, *Pittier 7990* (BR); *Utley & Utley 3876* (DUKE).

b. Anthurium pittieri var. **fogdenii** Croat, var. nov. Type: Costa Rica. Guanacaste: along the road between Santa Elena and Monteverde, ca. 2 mi from Santa Elena-Monteverde junction, elev. ca. 1,500 m, 10°20′N, 84°47′W, *Croat 47134* (MO-2769759, holotype; CR, K, SEL, US, isotypes; Live at MO).

Planta epiphytica, parva; caudex 3–6 cm longus, gracilis; lamina ovata-elliptica aut ovata, 4.5–8 cm longa, 2.3–3.5 cm lata, subcoriacea, epunctata, nervis supra leviter impressis subtus obscuris; inflorescentia effusa-erecta, foliis breviora; pedunculus 3.5–4.5 cm longus; spatha viridis, 2–3 cm longa, 6–9 mm lata; spadix viridis, 1.5–2.2 cm longus; antherae albae; baccae ignotae.

Epiphyte; stems 3–6 cm long, 0.7–1 cm diam.; roots green, moderately thin; cataphylls subcoriaceous, 1.5–2 cm long, rounded at apex, drying dark tan, splitting at base, persisting around stem. LEAVES spreading; petioles 1.3–7.3 cm long, 2–3 mm diam., terete, shallowly and sharply sulcate at base of blade; geniculum not apparent; blades ovate to ovate-elliptic, moderately thick, short-acuminate at apex, round to obtuse at base, 4.5–14 cm long, 2.3–4.7 cm wide, broadest at middle; upper surface glossy, lower surface semiglossy; midrib raised at base above, sunken in apical one quarter of blade, convexly raised below; primary lateral veins 5–10 per side, departing midrib at 50° angle, straight to collective vein, etched above, obscure below; lesser veins scarcely visible; collective vein arising near the base or from a primary lateral vein in the basal one half of blade, 2–4 mm from the margin. INFLORESCENCE erect-spreading, shorter than or as long as leaves; peduncle 3.5–11.5 cm long; spathe green (B & K Yellow-green 7/10), subcoriaceous, elliptic to obovate, 2–5.2 cm long, 6–15 mm wide, decurrent on petiole 0.8–1.5 cm, obtuse at base, short acuminate at apex, the apex tightly inrolled, the apiculum hooked toward spadix; stipe ca. 1 cm long; spadix green, 1.5–4 cm long, 3–4 mm diam. at base, 2–3 mm diam. at apex; flowers 4-lobed, ca. 2.5 mm long, 2.3 mm wide, the sides weakly to jaggedly sigmoid; ca. 3 flowers visible in the principal spiral, ca. 4 flowers visible in the alternate spiral; tepals matte, densely papillate, lateral tepals ca. 0.8 mm wide, the inner margin straight to convex; pistils weakly emergent; stigma minute, elliptic; stamens emerging from the base, lateral stamens emerging to midway before alternate stamens emerge at base; anthers white, ca. 0.4 mm in both directions, held over pistil in tight cluster; thecae ellipsoid, scarcely divaricate; pollen white. INFRUCTESCENCE not seen. Figs. 138 and 139.

Anthurium pittieri var. *fogdenii* is endemic to the vicinity of Monteverde (a biological preserve operated by the Tropical Science Center in San José), where it occurs with the typical variety of *A. pittieri*. The variety *fogdenii* is known only from the type locality in tropical wet or premontane wet forest life zones and is named in honor of Mike and Patricia Fogden who were kind enough to permit me to collect on their property near the Monteverde Preserve.

Anthurium pittieri var. *fogdenii* is distinguished by its small size, green spadix with white anthers, slender stems, and ovate to ovate-elliptic, subcoriaceous, epunctate leaf blades with etched veins on the upper surface and with obscure veins beneath.

The taxon differs from var. *pittieri* by having the veins prominently etched on the upper surface. This character disappears on drying so that in the dried condition it is not possible to sep-

arate the two taxa readily. Although *A. pittieri* is placed in section *Oxycarpium*, var. *fogdenii* looks much like members of section *Porphyrochitonium*, differing only in the absence of glandular punctations on the leaves.

COSTA RICA. GUANACASTE: between Santa Elena and Monteverde, *Croat 47134* (CR, K, MO, SEL, US); vicinity Monte Verde Preserve, *Croat 46771* (MO); PUNTARENAS AND ALAJUELA: in and around Monteverde Preserve, *Burger & Baker 9722* (F).

Anthurium pluricostatum Croat & Baker, Brenesia 16 (Supl. 1): 68. 1979. TYPE: Costa Rica. Limón: ca. 1 mile NE of Bribrí, ca. 40 miles SW of Limón (on coastal road); steep ravine above Río Catarata, elev. 50–100 m, *Croat 43243* (MO 2584480–81, holotype; CR, F, K, US, isotypes; Live at MO).

Terrestrial; stem 2.5–3 cm diam., to 23 cm long; leaf scars conspicuous, ca. 2.5 cm diam.; roots greenish, ca. 4 mm diam., moderately numerous and long, descending; cataphylls moderately thin, 6–12 cm long, acute to acuminate at apex, soon turning brown and weathering into a dense mass of persistent, coarse fibers. LEAVES with petioles erect, 26–68 cm long, 6–8 mm diam., subterete, narrowly flattened to weakly and obscurely sulcate adaxially, almost smooth to characteristically several-ribbed or -striate; geniculum 1.2–1.7 cm long; blades narrowly ovate, moderately thin, acuminate at apex, deeply lobed at base, 40–68 cm long, 20–38 cm wide, broadest near the point of petiole attachment, the margins broadly convex; anterior lobe 32–52 cm long, posterior lobes 10–19 cm long, directed downward or inward; the sinus spathulate, obtuse to rounded at apex; upper and lower surfaces semiglossy; midrib obtusely raised at base above, becoming acutely raised and then diminishing toward apex, prominently raised below; basal veins 3–6 pairs, 3 or 4 of them coalesced 3–4 cm, prominently raised above and below; the posterior rib thick, naked, almost straight, the outer margin flat or weakly rolled upward; primary lateral veins 6–9 per side, departing midrib at 30°–45° angle, almost straight to collective vein, raised near midrib but sunken towards apex above, raised below; interprimary veins usually few, scarcely raised above, flat below; secondary veins weakly sunken above, darker than surface and flat below; collective vein arising from the uppermost basal vein, 3–5 mm from margin, slightly sunken above, slightly raised and darker below. INFLORESCENCE erect-spreading, equalling or much shorter than the leaves; peduncle 17–43 cm long, 4–5 mm diam., terete to obscurely angular, sometimes heavily suffused with dark purple, 0.33–0.75 times as long as petioles; spathe subcoriaceous, pale purple-violet or green slightly suffused throughout with purplish-violet, especially on the inner surface (B & K Red-purple 7/7.5), oblong-lanceolate, 13–18.5 cm long, 2–3.7 cm wide, broadest in lower quarter, gradually long-acuminate at apex, rounded to obtuse at base, stiffly spreading, sometimes twisting, inserted at 50°–70° angle on peduncle; stipe ca. 9 mm long in front and 3 mm long in back, ca. 6 mm diam.; spadix pale lavender or green tinged with pale lavender (B & K Red-purple 8/10), yellowish-green near the tip or sometimes pale reddish-purple throughout (B & K Red-purple 3/5), 8.5–14.5 cm long, 7–9 mm diam. at base, 3–4 mm diam. at apex; flowers rhombic to weakly 4-lobed, 2.6–3.5 mm long, 2.4–3.6 mm wide, the sides straight to smoothly sigmoid, rarely jaggedly sigmoid; 7–9 flowers visible in the principal spiral, (8)10–15 flowers visible in alternate spiral; tepals semiglossy, papillate, with a few droplets when anthers are opening, the lateral tepals 1.3–1.8 mm wide, 3–5-sided, the inner margin straight or nearly so; pistils pale green becoming salmon-lavender (as tepals) with purplish dots, slightly mounded and weakly exserted above the tepals; stigma linear, 0.6–0.8 mm long, a pale, darker-edged slit, exuding droplets about 1 week before first stamens emerge, the nectar persisting even after all stamens are open; stamens emerging rapidly from the base, the lateral stamens emerging throughout before the alternate stamens begin to emerge at base, held just above the tepals in a circular cluster ca. 1.3 mm diam. (or sometimes only half emergent with the exposed part ephemeral); anthers white, 0.5–0.6 mm long, 0.9–1 mm wide, peeping out and opening while still small or the thecae standing on end, opening vertically and disintegrating when touched; thecae obovoid, slightly divaricate; pollen white. INFRUCTESCENCE with purplish berries, acute at apex. Figs. 143 and 152.

The species is known from Costa Rica, and in Panama in Chiriquí Province on the Burica Peninsula. It is certainly to be expected in Bocas del Toro Province as well. It occurs in a wide variety of life zones in Costa Rica, ranging from premontane wet transition forest to premontane wet and tropical wet forest at elevations from near

FIGURES 144–147. 144. *Anthurium podophyllum* (Cham. & Schlecht.) Kunth. *Hiwan 263.*—145. *Anthurium podophyllum* (Cham. & Schlecht.) Kunth (Cultivated at Antosh's).—146. *Anthurium prolatum* Croat & Baker. *Croat 47087.*—147. *Anthurium prolatum* Croat & Baker. *Croat 46979.*

FIGURES 148–151. 148. *Anthurium protensum* Schott, *Croat 47113*.—149. *Anthurium protensum* Schott, *Croat 35566*.—150. *Anthurium purpureospathum* Croat, *Croat 38094* (Type).—151. *Anthurium ramonense* Engl. ex K. Krause, *Croat 33984*.

FIGURES 152–155. —152. *Anthurium pluricostatum* Croat & Baker, *Croat 43205*.—153. *Anthurium purpureospathum* Croat, *Croat 38094*.—154. *Anthurium ramonense* Engl. ex K. Krause, *Croat 43340A*.—155. *Anthurium ranchoanum* Engl., *Croat 48519A*.

sea level to 1,000 m on both the Pacific and Atlantic slopes.

Anthurium pluricostatum is a member of section *Belolonchium* and is characterized by its terrestrial habit, subterete petiole with 7–10 low ridges, and spadix that is lavender to reddish-purple or green tinged with lavender, usually with a discolorous yellowish-green portion near the apex. The species is also unusual in having flowers with stigmatic droplets persisting while stamens emerge.

Anthurium pluricostatum is related to *A. ochranthum.* The latter species, although occurring in the same altitudinal range and life zones, has a very different inflorescence, including a bright yellow spadix (at anthesis), and stamens with pollen being extruded in slender ribbons. Both *A. pluricostatum* and *A. ochranthum* have a consistently terrestrial habit that is a diagnostic feature for species occurring at medium to low elevations (the character being of much less value in cloud forest regions).

Staminal dehiscence is somewhat variable. Usually the anthers are fully exserted although the filaments are not exposed. Sometimes (even in the same population) anthers are only about half emergent and the exposed portion of the thecae loses its form when the pollen matures.

The species displays an unusual pollination possibility since the stigmas produce copious droplets slightly before the stamens emerge, the droplets persisting until all anthers are open. Thus the species is only weakly protogynous and might best be considered homogamous. The behavior presents a clear possibility for self fertilization.

COSTA RICA. ALAJUELA: Finca Los Ensayos, NW of Zarcero, *Croat 43580* (MO). CARTAGO: Pacuare, Turrialba, *Ocampo 1432* (CR). LIMÓN: Hwy. between Siguirres and Limón, S of Siguirres, *Croat 43334* (MO); along Río Sixaola, E of Bratsi between Limón & Shirores, *Croat 43291* (MO); near Río Sixaola, SW of Bambu, NE of Bratsi, *Croat 43265* (MO); NE of Bribrí, SW of Limón, above Río Catarata, *Croat 43243* (CR, F, K, MO, US); along Río Catarata between Bribrí and Caribbean coast, *Croat 43205, 43206* (MO); near the Río Catarata in the hills between Bribrí on the Río Sixaola and the Caribbean costal plain, *Baker & Burger 64* (F); *106A* (CR, F, MO). PUNTARENAS: near Rincón de Osa, *Liesner 2209* (F, MO); Quebrada del Palo, *Croat 22604* (F); hills above Palmar Norte, *Croat 35103* (MO); *Utley & Utley 1109* (F). SAN JOSÉ: about 1 mile beyond divide between San Isidro del General and Dominical, *Croat 35269, 35324* (MO).

Anthurium podophyllum (Cham. & Schlect.) Kunth, Enum. Pl. 3: 80. 1841. *Pothos podophyllum* Cham. & Schlecht., Linnaea 6: 22. 1831. TYPE: Mexico. Veracruz: Hacienda de la Laguna, *Schiede & Deppe* (B; not seen, illustrated by Schott Aroid Drawing #791, W).

Pothos laciniatus M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10(1): 122. 1843. TYPE: Mexico. Veracruz: Zacualpan, *Galeotti 6055* (BR).

Anthurium polytomum Schott, Bonplandia 7: 337. 1859. TYPE: Mexico. (Photo of Schott Aroid Drawing #805, NYBG Neg. #N.S. 3924; Photo MO).

Anthurium pseudopodophyllum Schott, Bonplandia 7: 338. 1859. TYPE: Cultivated in Vienna (Photo of Schott Aroid Drawing #811, NYBG Neg. #N.S. 3926; Photo MO).

Anthurium ghiesbreghtii Linden ex Schott, Prod. Aroid. 538. 1860. TYPE: none listed.

Anthurium membranuliferum Schott & Ohlend. ex Engl., Monogr. Phan. 2: 196. 1879. (Known only in cultivation.)

Usually terrestrial or epipetric, often more than 1 m tall; stems 2.5–3.5 cm diam.; roots descending; cataphylls, coriaceous, 7.5–11 cm long, gradually acuminate at apex, drying medium brown, persisting as linear fibers. LEAVES with petioles erect-spreading, 39–69 cm long, ca. 9 mm diam., D-shaped; geniculum 5 cm long; blades subcoriaceous, broadly ovate, deeply to broadly lobed at base, (3)5–10 pedatisect, the lobes usually 5–12 pinnatifid, fused 8–10 cm at base, 16–47 cm long; the outermost lobes 7.5–27 cm long, auriculate; sinus hippocrepiform to nearly arcuate, rounded at apex; upper surface glossy, lower surface semiglossy; midrib of median lobe raised, rounded, diminished and flat at apex above, raised below; primary lateral veins 2–3 per side, departing midrib at 40° angle, sunken above, raised below; basal veins 3–5 pairs, second and third coalesced to 2 cm, the third and fourth coalesced 3.2 cm; the posterior ribs straight; collective vein arising from the first primary lateral vein, 8–9 mm from the margin, sunken above, raised below. INFLORESCENCE spreading-pendent, longer than leaves; penduncle 38–100 cm long, to 6 mm diam., terete, equal to or longer than petioles; spathe subcoriaceous, yellow-green (B & K Yellow-green 7/7.5), lanceolate, 4.5–9 cm long, 1.6–2.2 cm wide, broadest just above base, acuminate at apex, inserted at 45° angle on peduncle; stipe 9 mm long in front, 5 mm long in back, 4 mm diam.; spadix green, sometimes tinged with purple (B & K Yellow-green 6/5), 4–14 cm long, 7–11 mm diam. at base, 3–5 mm diam. at apex; flowers rhombic, 3.2–4.6 mm long, 2.5–4.6 mm wide, the sides straight to weakly sigmoid; 6–8

flowers visible in the principal spiral, 7–9 flowers visible in the alternate spiral; tepals matte, minutely papillate, lateral tepals 1.2–2.2 mm wide, the inner margins broadly rounded, turned up against pistils; pistil emergent, green; stigma linear, 0.6 mm long, dry, brown, crusty before stamens emerge; stamens emerging in a moderately slow sequence from base, exserted above pistil, then withdrawing, the leading stamens in any phase only a few spirals ahead of succeeding stamens; filament green; anthers white, held over pistil in tight cluster, ca. 0.6 mm in both directions; thecae narrowly ovoid, dark brown, slightly divaricate; pollen cream-colored. INFRUCTESCENCE pendent, spathe persisting; spadix to 4.5 cm diam.; berries dull orange (B & K Yellow-red 7/5), obovoid to obovoid-ellipsoid, rounded at apex, 13–19 mm long, 7–15 mm diam.; mesocarp thick, juicy, orange with small raphide cells; seeds 1 or 2, pale green, flattened, oblong to oblong-obovoid, 9–10 mm long, 5–6 mm wide, 3.3–4.3 mm thick (sometimes with one large almost subterete seed) with appendages at both ends, the lower appendage flattened, about as broad as the seed. Figs. 144 and 145.

Anthurium podophyllum is endemic to the Atlantic coast of Mexico in Veracruz and Oaxaca at elevations of 750 to 2,000 m in "selva mediana subperennifolia." The Oaxaca populations occur at higher elevations (up to ca. 2,000 m), and have leaf lobes mostly entire to sinuate, rarely lobed as in pre-adult plants of *A. podophyllum* from Veracruz. Veracruz populations usually occur below 1,000 m and have more finely dissected leaves with the lobes pinnatifid.

Anthurium podophyllum is in section *Schizoplacium* and is characterized by its subcoriaceous, pedatisect leaf blades with the lobes usually sinuate to pinnatifid, and by its long inflorescence usually equalling or exceeding the length of the leaves. The Oaxaca populations have leaves similar in shape to *A. pedatoradiatum*, but the latter is recognized by its much thinner leaf blades, lobes with uniform margins, and generally shorter peduncles.

The species is rare in the wild, having been collected in only a few relatively adjacent localities since the type collection was made in Zacualpan.

MEXICO. No other location, *Karwinski s.n.* (F); *Martens 137* (BR). OAXACA: between Teotitlán del Camino & Santa María Chilchotla, *Croat 48367* (MO). VERACRUZ: Barranca de Santa María, *Moore & Bunting 8852* (BH); Jalapa, *Sousa & Ramos 4744* (MEXU); Mirador, *Liebmann s.n.* (P); Municipio Totutla, *Ventura 3660* (ENCB); Zacualpan, *Galeotti 6013* (BR); *Purpus 6364* (MO, NY, UC, US); *Purpus 11130* (F, MO).

Anthurium prolatum Croat & Baker, Brenesia 16 (Supl. 1): 72. 1979. TYPE: Costa Rica. Heredia: Istaru Farm, Tirimbina, Sarapiquí; primary forest; 220 m elev., Sept. 1971, *Roy Lent 2140* (2 sheets) (F-1724125, holotype).

Epiphyte; stems 2–2.5 cm diam.; cataphylls thick, 30–36 cm long, subpersistent, acuminate at apex, drying tan, weathering into fibers at the base. LEAVES pendent; petioles 30–35 cm long, 6–8 mm diam., terete, sulcate; geniculum 1–1.2 cm long; blades strap-shaped, gradually long-acuminate at apex, narrowly acute at base, 108–142 cm long, 8–10 cm wide, broadest near the middle; midrib prominently raised above to very near the apex, raised below; primary lateral veins numerous, departing midrib at ca. 55° angle, scarcely or not at all distinguishable from the interprimary veins on upper surface, only slightly more prominent on lower surface; interprimary veins usually numerous; collective vein arising from near the base, 3–4 mm from margin throughout. INFLORESCENCE pendent; peduncle to 39 cm long, ca. 4 mm diam., slightly longer than petioles; spathe medium thick, pale green, spreading, lanceolate-linear, to 29 cm long, ca. 1.5 cm wide, broadest near base, acuminate at apex, acute at base, inserted at 70° angle on peduncle; spadix brown (fide label), to 60 cm long, 7–8 mm diam. at base, ca. 4 mm diam. at apex; the flowers (dry) rhombic, 3.4–4.5 mm long, 1.8–2.2 mm wide, the sides jaggedly sigmoid; 5–6 flowers visible in the principal spiral, 7–8 flowers visible in the alternate spiral; tepals smooth, the lateral tepals 2–2.5 mm wide, the inner margin convex; the pistil green, ca. 1 mm long, ca. 0.8 mm wide, emerging evenly throughout; the stigma ca. 0.7 mm long (dry), oblong; stamens perhaps only partly exserted above the tepals (at least partly retracted on drying). INFRUCTESCENCE pendent; berries probably orange. Figs. 146 and 147.

Anthurium prolatum is known only from northern Costa Rica in Alajuela and Heredia Provinces in tropical wet forest at 200 to 600 m elevation.

The species is a member of the section *Pachyneurium* and can be distinguished by the unusual, very long and narrow leaves, cataphylls, spadix.

and spathe. It is most easily confused with *A. protensum,* however, *A. prolatum* differs from that species by having its spadix more than twice as long as any observed for even the largest *A. protensum,* a spathe considerably more narrow and lacking the purple markings characteristic of *A. protensum,* and the flowers twice as long (0.5–2.5 mm long in *A. protensum,* 3.4–4.5 mm long in *A. prolatum*). In addition, the common *A. protensum* has not been collected below 1,000 m and is most common at 1,800 m elevation.

COSTA RICA. ALAJUELA: along Hwy. 15, between Naranjo and Aguas Zarcas, NE of Villa Quesada, *Croat 46979* (MO). CARTAGO: E of Cachí, *Croat 47087* (MO). HEREDIA: Istaru Farm, Tirimbina, Sarapiquí, *Lent 2140* (F).

Anthurium protensum Schott, Oesterr. Bot. Z. 8: 181. 1858.

Anthurium protensum. ssp. **protensum.** TYPE: Costa Rica. Heredia: Volcán Barba, 2,500–2,700 m, *Oersted 1992* (type not found; Photo of Schott Aroid Drawing #427, NYBG Neg. #N.S. 3848).

Anthurium joseanum Engl., Pflanzenr. IV 23B: 68. 1905. TYPE: Costa Rica. Cartago: Las Vueltas, Tucurrique, 635 m, *Tonduz 12818* (B, holotype; P, US, isotypes).

Anthurium costaricense Engl., Bot. Jahrb. Syst. 25: 398. 1898. TYPE: Costa Rica. Above Agua Caliente, 1,800 m, *Lehmann s.n.* (Drawing of Engler Arac. 274 at B, P).

Epiphyte, often pendent; stems short; cataphylls 12–22 cm long, drying tan, weathering into coarse fibers at base and persisting. LEAVES spreading-pendent; petioles 11–35 cm long, 5–7 mm diam., ± terete, sometimes flat or weakly sulcate adaxially; geniculum 1.5–2 cm long; blades strap-shaped 32–80 cm long, long-acuminate at apex, acute to rounded at base; upper surface matte to semiglossy, lower surface semiglossy; the midrib acutely raised above, convexly raised below; primary lateral veins numerous, sunken above, raised below; secondary veins distinct; collective vein arising from near the base, 4–5 mm from margin. INFLORESCENCE spreading-pendent, shorter than leaves; petioles 15–45 cm long, 6–7 mm diam.; spathe oblong-lanceolate, yellow-green to purple, usually at least tinged with purple, 10–15 cm long, 2.5–4 cm wide, usually held ± erect; spadix pale violet-purple, 8–12 cm long, 6–9 mm diam. at base, 2–4 mm diam. at apex; the flowers rhombic to 4-lobed, 2.5–2.7 mm long, 2–2.2 mm wide; 4–9 flowers visible in the principal spiral, 6–12 flowers visible in the alternate spiral; tepals matte; pistils green, emergent; stigmas with droplets 2–4 days before stamens emerge; stamens emerging from base, laterals first, preceding alternates by 2–3 spirals, held over pistil in a tight cluster; thecae brown, elliptic; pollen pale orange. INFRUCTESCENCE with spadix 14–32 cm long; berries orange, ± ovoid, weakly beaked, 11–13 mm long, 6–8 mm wide; seeds 2, pale brown, subovoid, weakly flattened, ca. 6 mm long, 4.5 mm wide, 3 mm thick. Figs. 148 and 149.

The species is found in Costa Rica and Panama from 635 to 2,700 m, principally in premontane rain and lower montane rain forest.

Anthurium protensum is a member of section *Pachyneurium* and is distinguished by its elongate, narrow leaf blades with many primary lateral veins, by its more or less terete petiole, and by its long, ovate to lanceolate spathe, pale violet-purple to lavender or greenish spadix and orange berries.

The species is closely related to *A. prolatum, A. brenesii,* and *A. seibertii,* all species with similar, elongate leaves. See the commentary following these species for distinguishing characteristics.

Anthurium protensum consist of two subspecies. The subspecies *protensum* occurs only in Costa Rica, while ssp. *arcuatum* Croat (ined.) occurs in Panama, ranging from Chiriquí to Veraguas at 1,300 to 1,750 m in premontane rain forest. The latter differs in being an erect plant with smaller leaves with fewer, more prominent sunken veins, an acute lower midrib, an arching inflorescence with shorter, usually ovate spathe, and a smaller spadix.

COSTA RICA. ALAJUELA & PUNTARENAS: Monteverde Nature Preserve, *Burger et al. 10792* (F). ALAJUELA: Zapote, *Smith 1268* (NY); vicinity Zarcero, *Croat 43533* (MO); *Austin Smith A692* (MO). CARTAGO: Carpintera, *Brade 2513* (BR); vicinity La Congreja, *Williams et al. 24182* (NY); NE of Pacayas, *Luteyn 3250* (DUKE); SE of Platanillo, *Croat 36714* (MO). GUANACASTE: La Palma, *Greenman & Greenman 5465* (MO); Monteverde, *Palmer 158* (NY); between Santa Elena and Monteverde, *Croat 47113* (MO). HEREDIA & SAN JOSÉ: Cerro de Zurquí, *Burger et al. 10290* (MO). HEREDIA: vicinity Bajo La Hondura, *Croat 44501* (MO); N of Concepción, *Primack et al. 276* (DUKE); Monte Cristo, *Rojas 513* (MO); near Rio Pará Blanco, *Lent 2874* (MO); N of Vera Blanca, *Croat 35566* (MO); *Maxon & Harvey 8304* (US); *Skutch 3652* (MO, NY); *3706* (MICH, US). PUNTARENAS: vicinity Jalaca Farm, Golfo Dulce Area, *Allen 5211* (US); Monteverde, *Ken-*

nedy 605 (US); *Luteyn 3406* (DUKE); SE of Santa Elena, *Almeda et al. 2031* (DUKE). SAN JOSÉ: between Aserri and Tarbaca, *Standley 41402* (US); Bajo La Hondura, *Lent 1446* (WIS); *Standley 36334* (US); La Palma, *Luteyn 3301* (DUKE); above Piedra, *Luteyn 3291* (DUKE); vicinity Vito San Cristóbal Sur, *Utley & Utley 3059* (MO).

Anthurium purpureospathum Croat, Selbyana 5 (3–4): 328. 1981. TYPE: Panama. Bocas del Toro: Station Milla 7.5 on Changuinola-Almirante Railroad, less than 100 m above sea level, along slender ridge to WW II communications facility, ca. 2 km NW of ruins of U.S. Army military barracks, *Croat 38094* (MO-2388335, holotype; CAS, F, K, MO, PMA, SEL, US; isotypes; Live at MO).

Epiphyte or terrestrial at higher elevations; stem hidden by roots; roots dense, 3–4 mm diam., descending; cataphylls coriaceous, 7–14 cm long, acuminate at apex, reddish, drying dark tan (B & K Yellow 5/2.5), subpersistent, remaining as reticulate fibers. LEAVES erect to spreading; petioles 12–31 cm long, 4–10 mm diam., ± quadrangular, flat to broadly and sharply sulcate, usually prominently 3-ribbed abaxially; geniculum 1–2.5 cm long; blades oblong-oblanceolate to oblong-elliptic, coriaceous, acuminate at apex, obtuse to acute or attenuate at base, 27–74 cm long, 7.5–40 cm wide, broadest at or above the middle; upper surface matte to semiglossy, lower surface glossy to semiglossy; midrib acutely raised above and below, diminishing at apex above; primary lateral veins (6)11–14 per side, departing midrib at 45° angle, raised in valleys above, raised below, arcuate-ascending, loop-connected in upper half; interprimary veins flat or prominulous above, prominulous below; secondary veins flat above and below; collective vein arising from one of the primary lateral veins near the middle, 4–8(13) mm from the margin, sunken above, raised below. INFLORESCENCE erect; peduncles 3–38 cm long, 0.8–2 cm diam., purplish or green, subterete, equal to or as long as petioles; spathe medium thick, purple to purplish with green mottling especially near base at center or green mottled with purple (B & K Red-purple 2/5) at anthesis, oblong to narrowly ovate, 4.5–17.5 cm long, 1.5–4 cm wide, broadest just above the base, cuspidate at apex, obtuse to rounded at base; spadix violet-purple (B & K Purple 2/7.5), (4)5–22 cm long, 1–2.5 cm diam. at base, 4–8 mm diam. at apex; flowers rhombic to weakly 4-lobed, 2–2.3 mm long, 2.5–3 mm wide, the sides gradually to jaggedly sigmoid; ca. 14 flowers visible in the principal spiral, ca. 7 flowers visible in the alternate spiral; tepals matte, with small scattered droplets, lateral tepals 1.4–1.6 mm wide, the inner margin flat against pistil; pistils slightly raised, purple becoming green and finally orange; stigma linear, ca. 5 mm long, with droplets for 4–10 days, drying with exserted papillae 4–6 days before first stamen emerges; stamens exserted ca. 1 mm, emerging in a slow progression from the base, the lowermost flowers with their full complement before the middle flowers have any stamens exserted, held in a tight, contiguous circle; filaments 0.2–1 mm long, flattened, transparent, tapered to anther, retracting to hold anther at edge of tepals; anthers ca. 0.7 mm in both directions; thecae ellipsoid, usually held closely parallel; pollen golden yellow (B & K Yellow 8/2.5), drying white. INFRUCTESCENCE erect to spreading; the spathe drying, usually persisting; spadix 9–19 cm long, to 4 cm diam.; berries narrowly ovoid, acute at apex with a round, minute, mammilliform style, orange, red-orange to red (B & K Red 6/7.5), to 10 mm long; the mesocarp pasty, transparent; seeds 1 or 2, ca. 4 mm long and 2 mm wide, pale greenish-yellow. Figs. 150 and 153.

The species is endemic to Panama and occurs principally from near sea level to 200 m in Bocas del Toro Province in wetter parts of tropical moist forest and premontane wet forest. It is to be expected in Limón Province in Costa Rica. A population on Cerro Colorado, in tropical wet or premontane rain forest at 1,200 to 1,500 m appears to differ in no way from the populations at lower elevations except that it has thicker leaves and consistently terrestrial habit. The terrestrial habit is not unusual for populations at higher elevations where a greater accumulation of debris exists and where the steeper slopes provide better drainage. The species should be expected at medium elevations as well.

Anthurium purpureospathum is distinguished by its rosulate habit, more or less oblanceolate leaf blades, almost quadrangular petioles often 3-ribbed abaxially, generally short peduncles, usually violet-purple reflexed spathe, usually short violet-purple spadix, early emergent pistils and long, sharply pointed, orange to red-orange berries.

The species is a member of section *Pachyneurium*, although the leaves sometimes have a collective vein arising from below the middle. It is closely related to no other known species.

Anthurium ramonense Engl. ex K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11: 611. 1932. TYPE: Costa Rica. Alajuela: at San Ramón, 1,200 m elev., *Tonduz 17703* (B, holotype; CR, isotype).

Anthurium isonervium Standl. & L. O. Wms., Ceiba 3: 104. 1952. TYPE: Nicaragua. Río San Juan: San Juan del Norte (Greytown), sea level, *Charles Smith 61* (EAP, holotype; MO, US, isotypes).

Epiphyte; stems short; roots pale green, in dense mass, ascending; cataphylls 8–11 cm long, coriaceous, drying brown, weathering into fibers and persisting at base of leaves. LEAVES erect-spreading; petioles subterete, narrowly and bluntly sulcate, 4–17 cm long, 4–7 mm diam.; geniculum 1.5–2 cm long; blades elliptic to broadly elliptic to obovate or oblanceolate, moderately thick, 22–54 cm long, 9.5–24 cm wide, abruptly acuminate at apex, acute to obtuse at base; semiglossy above and below, conspicuously punctate below; the midrib raised and ± flattened (sometimes shallowly sulcate near base) above, convexly to acutely raised below; primary lateral veins 15–18 per side, departing midrib at 45° angle, sunken above, raised below, straight to collective vein, loop-connecting with collective vein; lesser veins obscure; collective vein arising from base, 3–6 mm from the margin. INFLORESCENCE spreading-pendent, shorter or longer than leaves; peduncle 9–34 cm long, 3–9 mm diam., sometimes tinged reddish-violet, conspicuously ribbed beneath opening of spathe; spathe coriaceous, yellow-green sometimes suffused with purple, lanceolate or oblong, 6–12 cm long, 1.5–2.8 cm wide, short-acuminate at apex, obtuse to rounded at base, inserted at 40°–45° angle on peduncle; spadix green, tinged red-violet in later stages, 13–36 cm long, 5–11 cm diam. at base, 4–7 cm diam. at apex; flowers rhombic, 4–5 mm long, 3–3.5 mm wide, the sides straight to weakly sigmoid; 4–8 flowers visible in the principal spiral, 6–10 flowers visible per alternate spiral; tepals matte, minutely papillate, lateral tepals 2.5–3.5 mm wide, the inner margin ± straight; pistil emergent but not raised, pale red-violet; stigma greenish, linear, not conspicuously open; stamens emerging rapidly throughout, anthers barely visible at edge of pistil, soon retracting leaving only sparse amount of white pollen. INFRUCTESCENCE with spadix to 48 cm long, berries pale red, to faintly lavender or grayish-white, flattened at apex (depressed around style), 4–5 mm long, 5–7 mm wide (direction of axis), 4.5–5 mm wide (perpendicular to axis); seeds 3–4, greenish-white, 1.6–3 mm long, 1.3–2.1 mm wide, 1.2–1.5 mm thick; mesocarp juicy, gelatinous, translucent. Figs. 151 and 154.

The species is known from Nicaragua to Panama from sea level to 1,400 m elevation in wetter parts of tropical moist forest and in premontane wet, tropical wet, premontane rain, and lower montane wet forest life zones. In Costa Rica, the species is widespread on the Atlantic slope and rare on the Pacific slope. In Panama, the species is most abundant on the Atlantic slope but occurs also on the Pacific slope near the Continental Divide.

Anthurium ramonense is most closely related to *A. paludosum, A. durandii, A. alatipedunculatum* and *A. acutangulum,* which all share similar retracting stamens and densely punctate lower blade surfaces. *Anthurium ramonense* can be distinguished by a combination of its proportionally shorter, stouter petioles, generally larger blades and long, tapered, generally stout inflorescence. *Anthurium paludosum* differs in having thick, nondilacerating, persisting cataphylls and proportionally narrower, usually smaller, concolorous leaves with a conspicuous whitish-green midrib. *Anthurium durandii* differs in having proportionally longer petioles and in being geographically isolated in southwestern Costa Rica. *Anthurium alatipedunculatum* differs in having an alate peduncle and a 3-sided petiole. *Anthurium ramonense* is most easily confused with *A. acutangulum* because both share similar features including thin, dilacerating, promptly deciduous cataphylls and long inflorescences. *Anthurium acutangulum* differs, however, in having smaller, typically elliptic blades and a proportionally longer, more slender petiole. The petiole ranges from equally as long as the blade to one third as long as the blade in *A. acutangulum,* whereas the petiole of *A. ramonense* ranges from one sixth to one third as long as the blade. The spadix of *A. ramonense* is also proportionally longer and stouter than that of *A. acutangulum. Anthurium ramonense* is a member of section *Porphyrochitonium.*

Engler (1905) mentioned the affinity of *A. ramonense* with *A. filiforme* Engler of Colombia. This is perhaps another species in the complex but it is inadequately known at present.

COSTA RICA. ALAJUELA: N of Bijagua, *Croat 36502A, 36516* (MO); road from Cariblanco to Lake Hule, *Luteyn & Wilbur 4300* (DUKE); Lake María Aguilar, *Lent*

1530 (NY); from San Pedro to San Ramón, *Brenes 16171a* (NY); Santa María National Park, *Liesner 5156* (MO); N of Zapote, *Croat 46918* (MO); Zarcero, *Smith 865* (NY). CARTAGO: El Muñeco, *Luteyn 3233* (DUKE); between Moravia & Quebrada Platanillo, *Croat 36604, 36620, 36689* (MO); SE of Platanillo, *Croat 36814* (MO); Tapantí, *Valerio 1612* (F); Tucurrique, *Tonduz 12818* (US); W of Turrialba, *Croat 36831* (MO). HEREDIA: Puerto Viejo de Sarapiquí, *Croat 44302* (MO). LIMÓN: E of El Carmen, *Lent 2439* (MO); S of Siguirres, *Croat 43320* (MO). PUNTARENAS: SW of Cañas Gordas, *Croat 22278* (MO). SAN JOSÉ: between San Isidro del General and Dominical, *Croat 35446* (MO).

NICARAGUA. RÍO SAN JUAN: NE of El Castillo, *Neill 3331* (MO); San Juan del Norte (Greytown), *C. L. Smith 61* (GH). ZELAYA: Colonia Agrícola Yolaina, *Stevens 6309* (MO).

Anthurium ranchoanum Engl., Bot. Jahrb. Syst. 25: 421. 1898. TYPE: Costa Rica. Rancho Flores in territorio Bacha, Volcán Barba, 2,100 m, *Pittier 2295* (B, holotype; BR, G, isotypes).

Anthurium valerii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 137. 1937. TYPE: Costa Rica. Heredia: Vara Blanca, *Valerio 1600* (F, holotype).

Anthurium vinicolor Standl. & L. O. Wms., Ceiba 3: 106. 1952. TYPE: Costa Rica. San José: Cordillera de Talamanca near Copey, cloud forest, 1,800 m, 23 April 1949, *L. O. Williams 16538* (EAP, holotype; F, US, isotypes).

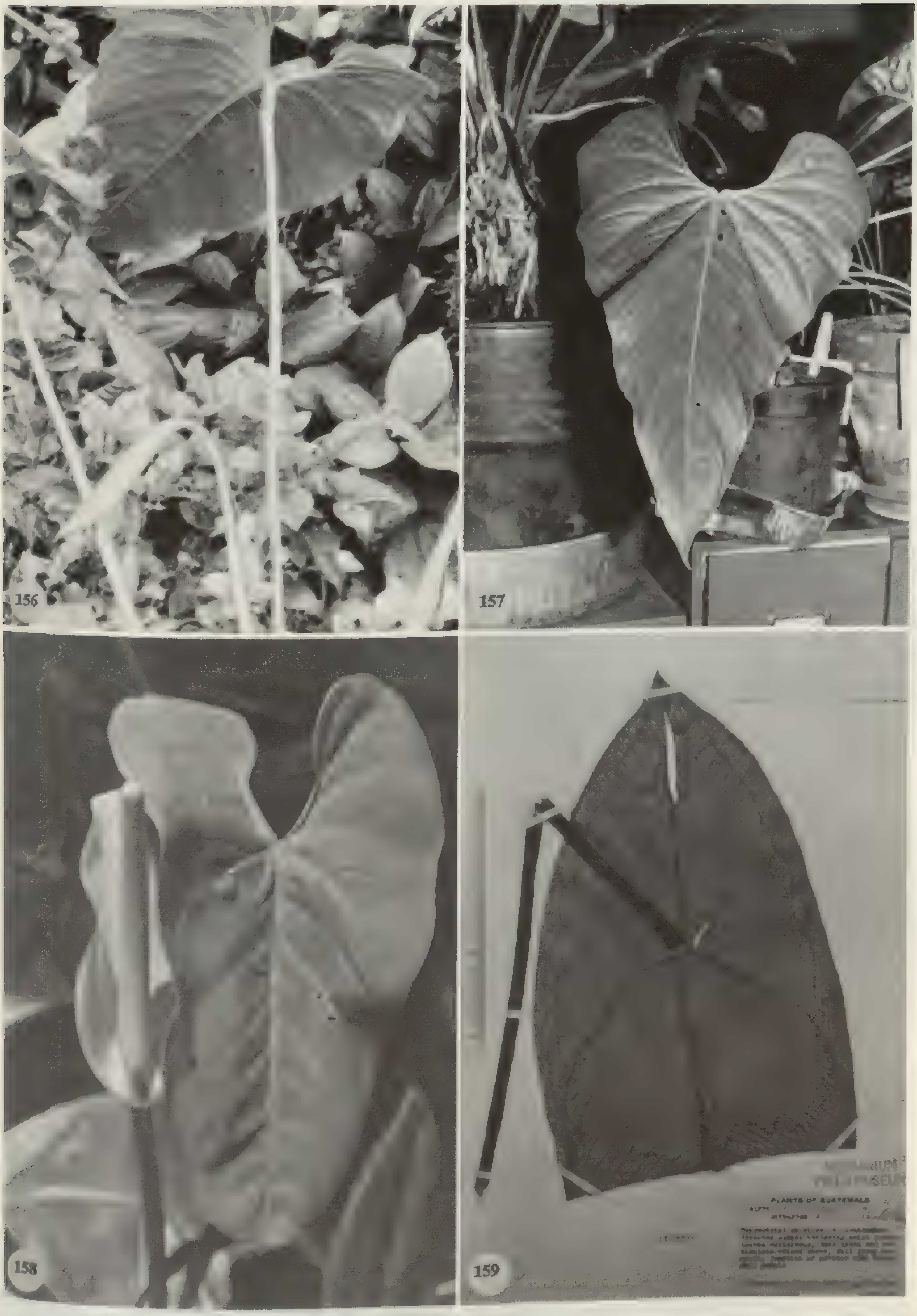
Epiphytic or terrestrial; roots thick, green, fuzzy, 3–7 mm diam., descending; cataphylls coriaceous, 13–30 cm long, apiculate at apex, drying tan (B & K Yellow-red 9/2.5), persisting intact at apex, splitting at base of leaves. LEAVES with petioles erect-spreading, subterete, shallowly and bluntly sulcate, 11–79 cm long, 5–15 mm diam.; geniculum 1.5–3 cm long; blades narrowly ovate or ovate-deltoid, moderately thick, acuminate at apex, shallowly to deeply lobed at base, 17–64 cm long, 9–34 cm wide, broadest between base and midway; the anterior lobe 12–29 cm long; the posterior lobe 7–13 cm long from sinus to outermost point; the sinus arcuate to parabolic; both surfaces semiglossy; midrib convexly raised above, diminished and sunken at apex, convexly raised below; primary lateral veins 4–9 per side, departing midrib at 40° angle, raised above and below; secondary veins conspicuous, sunken above, prominulous below; basal veins 3–6 pairs, the first pair usually free to the base, the third to sixth coalesced 1–2 cm, the fourth to sixth coalesced 3.5–6 cm; posterior rib naked, turned up; collective vein usually arising from one of the primary lateral veins, sometimes from the first basal vein, erect to weakly sunken above, raised below, 3–9 mm from margin. INFLORESCENCE erect-spreading, much shorter than leaves; peduncle 13–56 cm long; spathe subcoriaceous, lanceolate to narrowly ovate, green, tinged with purple on inner surface, 4–35 cm long, 2–6.5 cm wide; spadix sessile or with stipe 1.6–2.5 cm long, dark violet-purple, 3.5–19 cm long, 0.9–1.5 cm diam. at base, 6–9 mm diam. at apex; the flowers rhombic, 2–3.2 mm long, 2.6–3 mm wide, the sides jaggedly sigmoid; 5–10 flowers visible in the principal spiral, 7–20 flowers visible in the alternate spiral; tepals matte, lateral tepals 1–1.8 mm long; pistils green; stigma linear, ca. 0.5 mm long; lateral stamens emerging throughout, followed by alternates, exserted on flat filaments ca. 0.5 mm long, ca. 1 mm wide; anthers white, ca. 0.6 mm long, 0.7 mm wide; thecae ovoid-ellipsoid, slightly divaricate; pollen white. INFRUCTESCENCE arching-pendent; spadix to 50 cm long, to 3 cm diam.; berries orange, narrowly obovoid, acute at apex, to 14 mm long. Figs. 155 and 156.

Anthurium ranchoanum is found in Costa Rica and Panama at elevations of 500–2,300 m (usually above 1,000 m), usually in tropical wet, premontane rain, and lower montane rain forest life zones.

The species is an atypical member of section *Pachyneurium* and is recognized by its thick, ovate to ovate-triangular blades, with heavy, rather numerous veins, obtusely sulcate petioles; ovate to lanceolate, green, hooding spathe, tinged with purple; dark violet-purple, relatively stubby, scarcely tapered spadix with tight clusters of white stamens; orange berries; and especially by the fruiting spathe, which is stiffly erect. Also characteristic is the way the spadix is turned downward at anthesis. The source of the collective vein is variable, arising from first basal veins or, more frequently, in Costa Rica, from one of the primary lateral veins and, in Panama, from the first basal veins or primary lateral veins but more frequently from the lower basal veins.

The species is most easily confused with *A. cotobrusii*, which sometimes has similar leaves. The latter can be distinguished by its stiffly erect, conspicuously tapered spadix and prominently reflexed spathe.

The species is also related to *A. colonicum* K. Krause and *A. nervatum* Croat (ined.), both from Panama; and to *A. spectabile*, which ranges from Nicaragua to Costa Rica. The latter species has similar leaves (especially when dried) and a sim-



FIGURES 156–159. 156. *Anthurium ranchoanum* Engl., *Croat 48519A.*—157. *Anthurium ravenii* Croat & Baker. *Croat 32897.*—158. *Anthurium ravenii* Croat & Baker. *Croat 11529* (Type).—159. *Anthurium retiferum* Standl. & Steyerm., *Steyermark 51676.*

ilar inflorescence but differs in having usually more or less pendent leaves, and an elongate, more or less thin, spreading spathe, whereas *A. ranchoanum* has leaves more or less erect and a spathe that is more nearly ovate, thick, and stiffly erect. *Anthurium colonicum* has similar leaves but differs from *A. ranchoanum* in its reflexed and prominently undulate-margined and often contorted spathe, sharply protrudent, early emergent pistils, and narrowly oblong-elliptic, sharply pointed berries. *Anthurium nervatum* differs in having a reflexed spathe and a spadix that is usually much longer and more gradually tapered.

COSTA RICA. ALAJUELA: on road from Sucré to Lake Pozo Verde, *Luteyn et al. 4502* (DUKE). CARTAGO: near Copey, *Williams & Allen 16538* (US); SW of El Empalme, *Antonio 721* (MO). GUANACASTE: between Santa Elena and Monteverde, *Croat 47130* (MO). HEREDIA: S slopes of Cerros Caricias & Zurquí, *Luteyn 3275* (DUKE); NNE of Heredia, *Lellinger & White 981, 1012* (US); vicinity Cerro Chompipe, *Luteyn & Wilbur 4422* (DUKE); NE of Los Cartagos, *Lent 1898* (MO); Monte Cristo, *Rojas 511* (MO); on road to Sacramento, *Utley & Utley 4564* (DUKE); vicinity San Isidro, *Pittier 14058* (US); NE of San Isidro, *Standley & Valerio 50243, 50798, 51455, 51620, 52345* (US); N of San Rafael, *Lems s.n.* (K, NY); N of Vara Blanca, *Croat 36052, 36053* (MO); between Cerro Chompipe and Volcán Barba, *Baker 239* (MO); E slope of Volcán Barba, *Burger & Liesner 6369* (US); Volcán Barba, *Lems s.n.* (NY); *Pittier 2295* (BR); *Skutch 3657* (MICH, US). PUNTARENAS: Las Cruces Botanical Garden, *Croat 44443* (MO). SAN JOSÉ: NE of Cascajal, *Lent 2181* (MO); N of San Isidro del General, *Utley 407* (DUKE); S of Santa María de Dota, *Luteyn 3324* (DUKE); *Standley & Valerio 44077* (US); *Standley 41767* (US); Santa Rosa del Copey, *Tonduz 12266, 12267, 12269* (US).

Anthurium ravenii Croat & Baker, Brenesia 16 (Supl. 1): 75. 1979. TYPE: Panama. Panamá: north of Tocumen airport on road to Cerro Jefe, 2.5 miles north of Lago Cerro Azul, elev., ca. 700 m, *Croat 11529* (MO-2205477, holotype; F, K, PMA, US, isotypes; Live at MO).

Epiphyte; stem 1.5–2.5 cm diam., often to 40 cm long; the leaf scars almost contiguous, ca. 2 cm wide; roots relatively few, green to greenish-brown, 2–3 mm diam.; cataphylls subcoriaceous, to 17.5 cm long, drying brown, remaining intact, soon deciduous. LEAVES with petioles broadly and stiffly spreading, 19–70 cm long, 6–10 mm diam., subterete, obscurely and narrowly sulcate (the sulcus less than 1 mm wide); geniculum 2–2.5 cm long; blades moderately thick, ovate-triangular, narrowly to abruptly acuminate at apex, prominently lobed at base, 30–75 cm long, 16–40 cm wide, broadest at or near point of petiole attachment; the anterior lobe 25–44 cm long, the margin broadly rounded to weakly concave; the posterior lobes 10–19 cm long; the sinus spathulate, elliptic or obovate, acute, truncate or rounded at apex, usually broader than deep; the basal veins 5–9 pairs, the first and second free, the remainder coalesced 1–8 cm; the posterior rib curved, marginal to the sinus, 2.5–4.5 cm, the outer margin turned upward; blades semiglossy above, often broadly undulate, the lower surface semiglossy to matte; the midrib raised above and below; primary lateral veins 5–11 per side, departing midrib at 40°–50° angle, raised in valleys above, raised below; lesser veins conspicuous, flat above, weakly raised below; the collective vein arising from the first basal vein or one of the lowermost primary lateral veins, sunken above, raised below, 2–4 mm from margin. INFLORESCENCE erect-spreading; peduncles 15–40 cm long, 7–8 mm diam., terete, sometimes weakly ribbed on adaxial side, running the full length of the peduncle (continuous to the decurrent spathe); spathe greenish-white to pale green, sometimes tinged purplish at base, oblong-elliptic or ovate-elliptic, moderately thin, 8–18 cm long, 2.5–5.8 cm wide, broadest just above point of petiole attachment, abruptly acuminate at apex, the margins sometimes turned downward in lower half, rounded at base then decurrent to 15 mm; spadix cream, white, to pale green, usually sessile (rarely with a stipe 2–10 mm long), 8.5–24 cm long, 12–15 mm diam. at base, 10–12 mm diam. at apex; flowers weakly and irregularly 4-lobed, 2.2–3.5 mm long, 2.3–3.2 mm wide, sometimes conspicuously wider than long, the sides sometimes straight, usually jaggedly sigmoid; 8–12 flowers visible in the principal spiral, 8–15 flowers visible in the alternate spiral; tepals smooth, matte or weakly glistening with numerous minute droplets, the inner margins straight to convex, the lateral tepals 1.1–1.5 mm wide, 3-sided or more commonly 4-sided, with one lateral tepal acute on one end and obtuse on the other (proximal and distal ends), the opposite lateral tepal being a mirror image; pistil emergent but not raised, cream or whitish and difficult to discern from the adjacent tepals; stigma round, brushlike, somewhat elevated with short dense papillae, sometimes forming minute droplets about 7 days before first anthers emerge; the first stamens exposed in 2 or 3 days throughout spadix, all stamens emerged in about 10 days after

first appears, usually exserted above the tepals, 1.2–1.5 mm, held in a very tight cluster; filaments flattened, fleshy, 0.6–0.8 mm wide, slightly longer than the anther, sometimes retracting but usually remaining exserted, drying and twisting; anthers white, 0.5–0.6 mm long, 0.6–1 mm wide; thecae not divaricate; pollen pale lemon-yellow, fading dirty white. INFRUCTESCENCE arching-pendent; the spathe usually deciduous; spadix 14–44 cm long, ca. 2.5 cm diam. (with berries emerged); berries usually evenly emerged (even before maturity), narrowly ovoid, acute at apex, bright red, usually white in lower half; mesocarp gelatinous, transparent; seeds 2, white to brown with white punctations, green at apex, flattened, broadly elliptic, 3.7–4 mm long, 2.5–2.7 mm wide, ca. 2 mm thick. Figs. 157 and 158.

Anthurium ravenii ranges from Honduras to the Pacific slope of Ecuador. It usually occurs in tropical wet and premontane wet forest from near sea level to 1,000 m elevation, but it has also been found in tropical moist forest in Darién Province in Panama.

The species is a member of section *Calomystrium* and is unusual in having an orbicular, brushy, elevated stigma rather than a slitlike depressed stigma (in dried material a darkened slitlike area becomes visible). Distinguishing features include major veins that dry reddish-brown, the weak and brittle spathe, the scarcely tapered, whitish spadix, the usually long-exserted stamens, and bright red berries. The species is not close to any other species although for many years material of this species was called *A. concinnatum*, a completely unrelated species of higher elevations.

COSTA RICA. No other location, *Winters 9928* (US). ALAJUELA: N of Bijagua, *Utley & Utley 5310* (DUKE); between San Lorenzo and Bajo Rodríguez, *Utley 4612* (DUKE); near Quebrada Guillermina, N side of Volcán Arenal, *Lent 3409* (F, NY); road from Cañas to Upala, N of Bijagua, *Croat 36425* (MO); S of Canalete near the Río Zapote and along the new road to Upala, *Burger & Baker 9975* (F, MO). GUANACASTE: slopes of Volcán Miravalles, above Río Naranjo, *Primack, Stone & Luteyn 446* (DUKE); Río Naranjo forest, *Pittier 7541* (B). LIMÓN: 2.5 km east of Guapiles, *Jiménez 2093* (NY); Río Hondo, plains of Santa Clara, *Cook & Doyle 514* (US); Hacienda Tapezco, Hacienda La Suerte, W of Tortuguero, *Davidson 6871, 7020* (LA). PUNTARENAS: between Puerto Cortez and Palmar Norte, *Jiménez 2241* (CR, F); vicinity Palmar Norte, *Croat 35209* (MO); *Allen 5245* (EAP, F, US); E of Las Cruces on Property of R. Wilson, *Burger & Matta 4435* (F); Corcovado National Park, *Liesner 2901A* (MO); W of Rincón de Osa, *Burger & Stolze 5445, 5465* (CR, F); *Raven 21531* (DH, F); *Burger & Liesner 7200* (CR, F, US); *Burger & Gentry 8868* (F), *8981A* (F, MO); Playa Blanca near Rincón de Osa, *Liesner 2178* (MO, US); Rincón de Osa, region SW of airstrip, *Utley & Utley 1058* (CR, F, MO, SEL), *1106, 1120* (F); Vicinity San Vito de Java, *Croat 32897* (MO). SAN JOSÉ: road between San Isidro del General and Dominical, SW of Río Pacuare, *Croat 35213, 35265, 35338* (MO).

HONDURAS. ATLANTIDA: vicinity La Ceiba, *Yuncker et al. 8741* (NY).

NICARAGUA. RÍO SAN JUAN: valley of Río Indio, *Neill 1550* (MO); Río San Juan, near Caño Chontaleño, NE of El Castillo, *Neill 3418, 3621* (MO).

Anthurium retiferum Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 211. 1947. TYPE: Guatemala. Huehuetenango: Sierra de los Cuchumantes, Cerro Huitz, between Nimahuitz and Yolhuitz, elev. 1,500–2,600 m, *Steyermark 48621* (F, holotype).

Terrestrial or epiphytic. LEAVES with petioles 26–37 cm long, 6–8 mm diam., flattened adaxially with sharp margins, terete abaxially; geniculum 1.5 cm long, dull purple; blades coriaceous, narrowly to broadly oblong-elliptic, 33–47 cm long, 12–22 cm wide, broadest just below middle, short-acuminate at apex, truncate to round at base; both surfaces semiglossy; midrib raised above and below, red-violet above; basal veins 1–2 pairs; primary lateral veins 6–12 per side, departing midrib at 40°–50° angle, equally as prominent as the basal veins, all veins drying prominently raised above and below; collective vein arising from one of the primary lateral veins, ca. 1.5 cm from margin. INFLORESCENCE with peduncle 19 cm long, 4 mm diam., peduncle and spathe red-violet; spathe lanceolate, reflexed, ca. 6.5 cm long, 1.3–1.5 cm wide, cuspidate-acuminate at apex; spadix sessile, dull purple, 8.5–9 cm long, 4–5 mm diam. at base, 3–4 mm diam. at apex. INFRUCTESCENCE unknown. Fig. 159.

Anthurium retiferum is endemic to Guatemala in the Sierra de los Cuchumantes in the Department of Huehuetenango at 1,500 to 2,600 m.

The species is in section *Belolonchium* and is characterized by its sessile, purplish spadix and its coriaceous, oblong-elliptic leaf blades with the primary lateral veins equally as prominent as the basal veins and with prominently raised tertiary veins (on drying).

The species is perhaps closest to *A. parvispathum* but differs in having much broader leaves and in having the tertiary veins prominently raised on drying.

GUATEMALA. HUEHUETENANGO: Cerro Huitz, between Nimahuitz and Yolhuitz, *Steyermark 48621* (F); Cerro Negro, E of Las Palmas, *Steyermark 51676* (F, US).

Anthurium riograndicolum Matuda, Anales Inst. Biol. Univ. Nac. México 27: 347. 1957. TYPE: Mexico. Oaxaca: between La Gloria and Río Grande, *MacDougall s.n.* (MEXU, holotype).

Terrestrial; stems 2 cm diam. or larger; cataphylls triangular, drying reddish-brown, weathering into moderately thin longutudinal fibers. LEAVES with petioles to 50 cm long, 7–9 mm diam., bluntly sulcate adaxially; geniculum 1.5 cm long, thicker than petiole, obtusely and narrowly sulcate; blades coriaceous, narrowly ovate, acute at apex with short apiculum, deeply lobed at base, to 35 cm long, 22.5 cm wide, broadest just below point of attachment; the anterior lobe 25.5 cm long; the posterior lobes 12.5 cm long from apex of sinus to tip of lobe; sinus obovate, rounded at apex; upper surface semiglossy, with sparse glandular punctations, lower surface semiglossy with dense glandular punctations (the punctae irregular, to 0.4 mm diam.); the midrib prominently raised above, diminished and sunken at apex, sharply raised below; basal veins 5–6(7) pairs, the 4–5(6)th coalesced ca. 3.5 cm; posterior ribs slightly curved, the outer margin curled up and inward; the primary lateral veins 4–5 per side, scarcely visible, departing midrib at 50° angle, curved to the collective vein, raised below, interprimary veins scarcely less prominent than primary lateral veins; collective vein arising from one of the basal veins, 2–10 mm from margin. INFLORESCENCE erect-spreading (?); peduncle to 69 cm long, 7 mm diam., terete, longer than petioles; spathe subcoriaceous, green tinged with purple, oblong-lanceolate, to 11.5 cm long, to 1.2 cm wide, broadest just above the base, meeting on peduncle at ca. 90° angle; spadix sessile, to 17.5 cm long, to 1 cm diam. at base, to 4 mm diam. at apex; flowers rhombic, 3.7–4 mm long (dry), 2.7–3 mm wide (dry), the sides straight to sigmoid; 8–10 flowers visible in the principal spiral, 6–7 flowers visible in the alternate spiral; lateral tepals ca. 2 mm wide (dry), the inner margins concave; pistils weakly emergent; the stigma ellipsoid, 1 mm long; stamens exserted just above edge of tepals; anthers held at edges of pistil, 0.5 mm long (dry), 0.7 mm wide; thecae broadly elliptic, scarcely divaricate; pollen not seen. INFRUCTESCENCE not seen. Fig. 160.

Anthurium riograndicolum is known only from the type specimen collected perhaps in eastern Oaxaca, although no typical aroid collecting area is represented there. The notes by MacDougall attribute the collection from between "La Gloria and Río Grande." There are a number of towns with either name in Oaxaca.

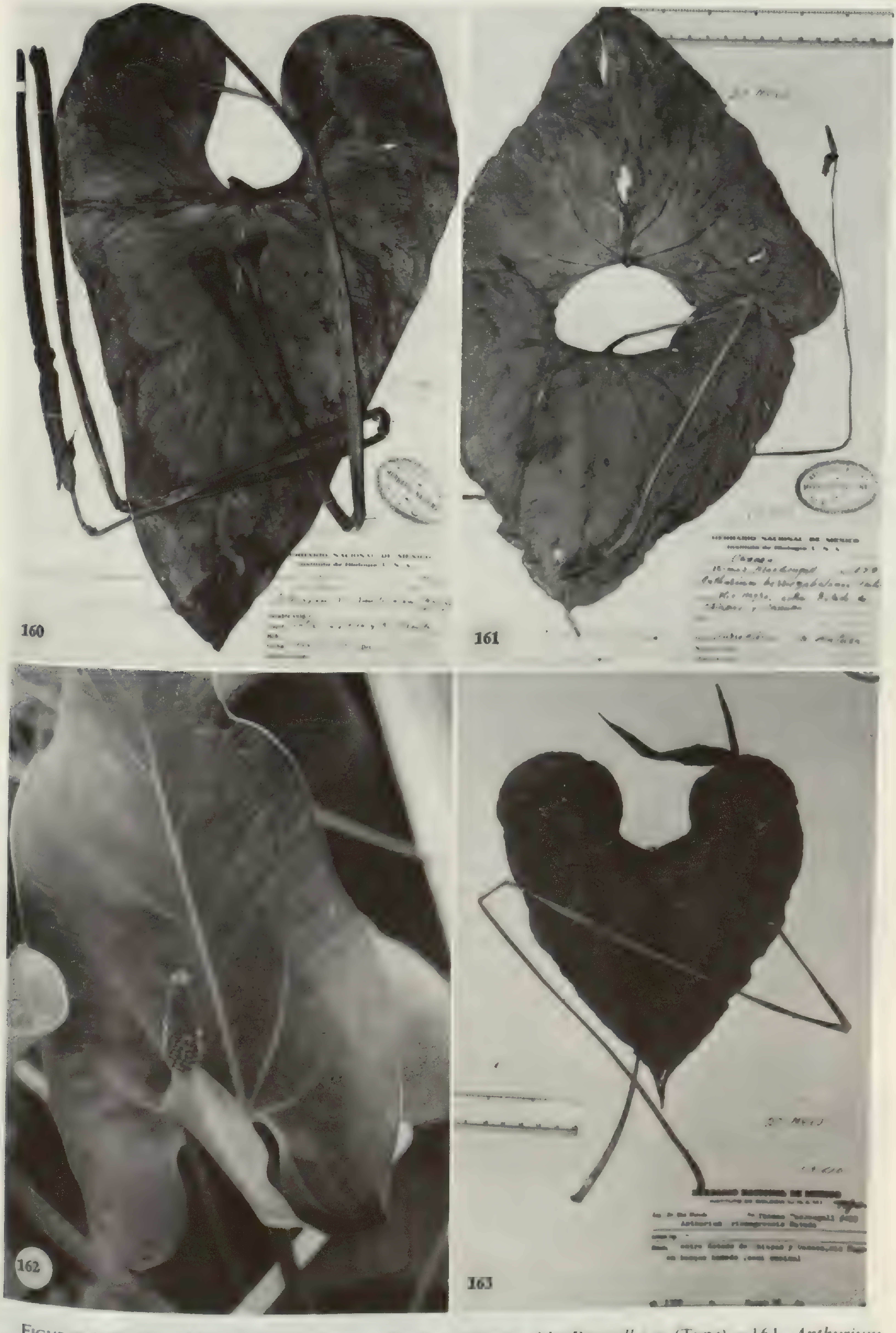
The species is a member of section *Belolonchium* and is distinguished by its coriaceous, ovate, glandular-punctate blade with an acute apex and conspicuous posterior lobes with an obovate sinus.

The species resembles *A. rzedowskii*, which also has thick, ovate, lobed leaves but that species has a much broader spathe and lacks glandular punctations. *Anthurium riograndicolum* is probably most closely related to *A. lucens* and may prove to be inseparable from it, but the species is currently represented by only the incomplete type specimen that differs from *A. lucens* primarily in having thicker blades that are acute rather than acuminate at the apex.

MEXICO. OAXACA: between La Gloria & Río Grande, *MacDougall s.n.* (MEXU).

Anthurium rionegrense Matuda, Anales Inst. Biol. Univ. Nac. México 36: 109, Fig. 4. 1966. TYPE: Mexico. Oaxaca: Río Negro between the states of Chiapas and Oaxaca, *MacDougall 459* (MEXU).

Epiphyte; stems short. LEAVES with petioles 19–28 cm long, sulcate adaxially; the geniculum 1.5 cm long; blades subcoriaceous, ovate, 20–22 cm long, 16–23 cm wide, gradually acuminate at apex, broadly lobed at base, broadest at point of petiole attachment; the anterior lobe 14–15 cm long; posterior lobes 7–9 cm long; sinus hippocrepiform, rounded at apex; midrib raised above and below; basal veins 4–6 pairs, fourth to sixth coalesced 1.5–2.1 cm; posterior ribs naked; primary lateral veins 2–4 per side, departing midrib at 50° angle, raised above and below; collective vein arising from first basal vein, 8–10 mm from margin. INFLORESCENCE longer than leaves; peduncle terete, 27–61 cm long; spathe linear-lanceolate, 2.5–8.5 cm long, 5–12 mm wide, broadest below middle, acuminate at apex, clasping at base; spadix green, 2–5 cm long, 3–5 mm diam. at base, 2 mm diam. at apex; the flowers rhombic, 4 mm long, 2.8 mm wide, the sides straight; 4 flowers visible in the principal spiral, 5 flowers visible in the alternate spiral; tepals



FIGURES 160–163. 160. *Anthurium riograndicolum* Matuda, *MacDougall s.n.* (Type).—161. *Anthurium rionegrense* Matuda, *MacDougall 459* (Type).—162. *Anthurium rzedowskii* Croat, *Croat 45520*.—163. *Anthurium rionegrense* Matuda, *MacDougall 459* (Type).

punctate, lateral tepals 1.5 mm wide, inner margin convex, turned up; pistil emergent, green; stigma slitlike, 7 mm long; stamens held over pistil; anthers cream, ovoid, 3 mm long, 4 mm wide; thecae ellipsoid, scarcely divaricate. INFRUCTESCENCE not seen. Figs. 161 and 163.

Anthurium rionegrense is known only from the Río Negro and Río Mono Blanco in the vicinity of the Oaxaca and Chiapas frontiers. Neither location has been located so the elevation is uncertain, but most elevations along the western Chiapas border range from 200 to 1,000 m, and only Cerro Baúl on the Oaxaca border, southwest of Cintalapa, is very high, extending up to about 1,800 m.

The species is a member of the section *Belolonchium* and is recognized by its thin, broadly ovate leaves with short, linear raphide cells visible on the upper surface on drying and by its slender tapered, greenish spadix with the tepals thin and clear along the inner margins and otherwise distinctly punctate with raphide cells.

Anthurium rionegrense is perhaps most easily confused with two other thin leaved, basically ovate-cordate species, *A. ovandense* and *A. lezamae*. *Anthurium ovandense* differs in having the anterior lobe usually concave along the margins whereas *A. lezamae* differs in being more narrowly ovate and in having an alveolate epidermal pattern on drying.

MEXICO. OAXACA: Río Negro, between Chiapas and Oaxaca, *MacDougall 459* (MEXU); Río Mono Blanco, *MacDougall 7940* (MEXU).

Anthurium rzedowskii Croat, sp. nov. TYPE: Mexico. Guerrero: along road between Hwy. 95 near Milpillas and 3.5 mi west of junction with road to Chichihualco, elev. 2,425 m, *Croat 45520* (MO-2690028–31, holotype; Live at MO).

Planta epiphytica aut terrestris; caudex ad 30 cm longus, 2–3 cm diam.; lamina ovata aut ovata-triangularis, 24–64 cm longa, 15–46 cm lata, basi cordata coreacea, nervo collectivo plerumque e nervo basi primo aut interdum e nervo laterali exorienti, saepe nervo collectivo secondario; inflorescentia effusa-erecta, foliis breviora; spatha viridis, 3.5–13 cm longa, 1.6–6 cm lata; spadix viridis, 3.8–13 cm longus; baccae immaturae purpureae.

Epiphytic or terrestrial; stems green, less than 30 cm long, 2–3 cm diam.; leaf scars 1.5 cm wide; roots 5–6 mm diam., pale green to tan, descending; cataphylls subcoriaceous, 6–10 cm long, pale green, acute at apex with slender subapical apiculum to 3 mm long, drying dark brown, the apex remaining intact, splitting at base and persisting. LEAVES with petioles erect to spreading, subterete or flattened adaxially, rarely with single abaxial rib; geniculum 2–2.5 cm long; blades ovate to ovate-triangular, acuminate at apex, shallowly to deeply lobed at base, 24–64 cm long, 15–46 cm wide, broadest below middle or near point of petiole attachment; anterior lobe 16–49 cm long, the margins convex; posterior lobes 7–20 cm long; sinus arcuate to parabolic, frequently with decurrent petiole; upper surface semiglossy, lower surface matte to semiglossy; the midrib flat to weakly, convexly raised above, narrowing and sunken at apex, prominently raised below; basal veins 3–7 pairs, the first free, the remainder coalesced 1–3.5 cm, the fourth to sixth sometimes coalesced up to 6 cm, raised above, prominulous below; primary lateral veins 7–17 per side, departing midrib at 35°–65° angle, weakly raised in valleys or sunken above, raised below, straight to weakly curving to collective vein; interprimary veins flat above, prominulous below; collective vein 1.5–3.5 mm from the margin, arising from the first basal vein, frequently with a secondary collective vein 0.4–1 mm from the margin, arising from the second basal vein and extending irregularly to apex or running to margin in apical quarter of blade, sunken above, raised below. INFLORESCENCE erect-spreading, shorter than leaves; peduncle 19–56 cm long, 4–7 mm diam., terete; spathe moderately thick, medium green (B & K Yellow-green 7/7.5), narrowly to broadly ovate, 3.5–13 cm long, 1.6–6 cm wide, abruptly acuminate at apex, rounded at base, inserted at 80°–90° angle on peduncle; stipe 9 mm long in front, 5 mm long in back; spadix green (B & K Yellow-green 7/7.5), 3.8–13 cm long, 8–10 mm diam. at base, 6–9 mm diam. at apex; the flowers rhombic to sub-4-lobed, ca. 2.3 mm long, ca. 2.9 mm wide, the margin ± obscure, straight to weakly sigmoid; 6–7 flowers visible in the principal spiral, 8–9 flowers visible in the alternate spiral; tepals matte, densely and minutely papillate, small droplets on tepals as stamens emerge, lateral tepals ca. 2.1 mm wide, the inner margin broadly rounded; pistils weakly emergent before stamens emerge, green, darker than tepals and conspicuously punctate; stigma linear, ca. 0.5 mm long, nearly obscure; stamens emerging from the base in a rapid sequence, the lateral stamens emerging first, quickly followed by alternates; the anthers creamy white usually

not opening until the third or fourth stamens emerge, exserted briefly on translucent filament, held inward over pistil, ca. 1.1 mm long, ca. 1.2 mm wide; thecae oblong-ovoid, slightly divaricate; pollen creamy white, fading to white. INFRUCTESCENCE pendent; spathe persisting; immature berries purplish, round at apex, mature berries not seen. Figs. 162 and 164.

Anthurium rzedowskii is known only from Mexico in the states of Guerrero, Oaxaca, and Chiapas at elevations of 1,400 to 2,900 m in "bosque pino-encino." It is named in honor of Dr. J. Rzedowski of the Instituto Polytechnica in Mexico City, one of the first collectors of the species.

The species is a member of section *Belolonchium* and is characterized by its coriaceous, ovate blades with the collective vein usually arising from the first basal vein or sometimes arising from one of the primary lateral veins and frequently with a secondary collective vein extending irregularly along the margin to the apex or almost to the apex.

It is probably most similar to *A. subcordatum* in having coriaceous leaf blades with the collective vein arising from the first basal vein or one of the primary lateral veins, and in frequently having a secondary collective vein arising from the second basal vein and extending along the margin to the apex or almost to the apex. *Anthurium subcordatum* differs in having truncate to subcordate leaf blades, a violet-purple spadix; it occurs in Guatemala, El Salvador, and Honduras.

MEXICO. CHIAPAS: Municipio of Siltepec, *Breedlove & Smith 31867* (DS); *Croat 47367* (MO); *Matuda 38524* (DS, MEXU). GUERRERO: between Milpillas and Atoyac de Alvarez, *Croat 45520* (MO); Municipio of Tlacotepec, *Rzedowski 16528* (ENCB, MICH); Omiltemi, *Lachica s.n.* (ENCB); Sierra Madre del Sur along the Milpillas-Atoyac Road, *Reveal et al. 4252, 4331* (US). OAXACA: between Oaxaca and Pochutla, *Croat 46056, 46188* (MO).

Anthurium salvadorense Croat, Selbyana 5 (3–4): 333. 1981. TYPE: El Salvador. Ahuachapán: 1.5 miles SW of Tacuba on road to San Francisco Menéndez; riverbank, Rió Chokama, 700 m elev. *Croat 42169* (MO-2583750, holotype; CAS, F, ITIC, K, SEL, US, isotypes; Live at MO).

Terrestrial or rupicolous; stems 2–3 cm diam., usually well rooted; roots to 1 cm thick, descending; cataphylls moderately thick, 5–8 cm long, apiculate at apex, pale green, drying light brown (B & K Yellow 5/5), persisting intact or dilacerating. LEAVES erect-spreading; petioles ± quadrangular, 11–22 cm long, 6–8 mm wide, broadly rounded to slightly 3-ribbed abaxially, broadly and sharply sulcate, sometimes with a medial rib; geniculum 1–1.5 cm long; blades elliptic to oblanceolate, medium thick, gradually acuminate at apex, turned downward (the acumen ca. 1.5 cm long), obtuse to rounded and auriculate at base, 25–50 cm long, 8–26 cm wide, broadest at or above the middle; upper surface matte to semiglossy, lower surface matte; midrib obtusely raised above, diminishing and sunken at apex, convexly raised below, ribbed near base; primary lateral veins 8–14 per side, departing midrib at ca. 45° angle, raised at midrib, diminishing and sunken near margin above, prominently raised below, straight to near margin, loop-connected in upper half; lesser veins flat above, raised below; collective vein arising from middle or above, ca. 5 mm from margin, sunken above, raised below. INFLORESCENCE erect-spreading; peduncle 13–45 cm long, 5–7 mm diam., faintly striate, 1-ribbed adaxially and sometimes abaxially, longer than petioles; spathe ovate-lanceolate, medium thick, pale green (B & K Yellow-green 8/10), held erect, enshrining and wrapped around base of spadix, 4.5–6.5 cm long, 2.4–2.7 cm wide, broadest just above base, narrowly acute, inserted at 10°–25° angle on peduncle; spadix pale green (B & K Green 8/5), 2.5–6.5 cm long, 8–12 mm diam. at base, 4–7 mm diam. at apex, held at a slight angle from the peduncle; flowers ± irregularly 4-lobed, 2–3.3 mm long, 2.5–3.6 mm wide, the sides jaggedly sigmoid; ca. 10 flowers visible in the principal spiral, ca. 9 flowers visible in the alternate spiral; tepals matte, densely papillate, lateral tepals 1.4–1.7 mm wide, turned up against emerging pistil; pistils weakly emergent, green; the stigma elliptic, ca. 0.4 mm long, erect and brushlike, with a small droplet apparent 2–4 days before first stamens emerge; stamens emerging rapidly in a complete progression from the base, lateral stamens emerging at apex when the third and fourth stamens are emerging at the base; anthers pale green, 0.8–1.2 mm long, 0.7–1.3 mm wide, held in a close, contiguous circle around and over the stigma, held at about the same height as the style; thecae weakly divaricate; pollen pale yellow, soon fading white. INFRUCTESCENCE spreading; spathe persisting and erect; the spadix to 9 cm

FIGURES 164–167. 164. *Anthurium rzedowskii* Croat, *Croat 47367*.—165. *Anthurium salvadorense* Croat, *Croat 42169* (Type).—166. *Anthurium salviniae* Hemsl. (Cultivated at Selby Gardens).—167. *Anthurium salviniae* Hemsl., *Croat 36480*.

long, ca. 2 cm diam.; berries broadly obovoid, 5.5–9 mm long, 4–9 mm wide, rounded to flat or weakly indented at apex, orange-red (B & K Yellow-red 5/2.5 to Red 4/10); pericarp moderately thick, with dense punctiform raphide cells, especially in apical half; mesocarp pulpy or mealy with numerous raphide cells; seeds 1 or 2, obovoid to broadly obovoid, yellowish-white to tan, 6–6.5 mm long and 5–5.8 mm wide, 3 mm thick, densely covered with punctiform raphide cells. Figs. 165 and 168.

Anthurium salvadorense is known only from El Salvador and Guatemala at 500 to 800 m elevation. It was first collected by Sisto Alberto Padilla in 1922 in the Department of Ahuacapán in El Salvador. The species was later collected by Paul C. Standley in the adjacent Department of Jutiapa in Guatemala.

The species is a typical member of section *Pachyneurium* and the earlier collections were confused with *A. schlechtendalii,* to which it is related. *Anthurium salvadorense* is distinguished by being usually a well rooted plant with fewer, very large fleshy roots and a usually almost elliptic blade, but especially by its inflorescence, which has a pale green, ovate-lanceolate spathe that is weakly convolute at the base and erect, enshrining the usually short, pale green spadix. *Anthurium schlechtendalii* differs in having usually oblanceolate blades, a coriaceous, more lanceolate, prominently reflexed, usually purplish spathe, and a more elongate, purplish spadix.

EL SALVADOR. AHUACHAPÁN: no other locality, *Padilla 296* (US); El Imposible, vicinity San Francisco Menéndez, *Bernhardt s.n.* (MO); *Croat 42092* (MO), *42169* (CAS, F, ITIC, K, MO, SEL, US).
GUATEMALA. JUTIAPA: vicinity Jutiapa, *Standley 76313* (F, US); SW of San Cristóbal, *Dunn et al. 23222* (UMO). ZACAPA: road to Finca Agua Fría, *Croat 41879* (F, MO).

Anthurium salviniae Hemsl., Diagn. Pl. Nov. Mexic. 36. 1878. TYPE: Guatemala. Volcán de Fuego, *Salvin s.n.* (K).

Anthurium giganteum Matuda, Madroño 10: 169. 1950, non Engl., 1898. *Anthurium enormispadix* Matuda, Revista Soc. Mex. Hist. Nat. 11: 94. 1950. TYPE: Mexico. Chiapas: Escuintla, Salto de Agua, *Matuda 18043* (MEXU, holotype; UC, isotype).

Robust rosulate epiphyte, rarely on rocks; stems short with mass of thick roots; cataphylls thick, fist-like, cucullate, rounded at apex, drying brown, remaining intact, ultimately becoming fibrous at base. LEAVES erect; petioles flattened or sulcate adaxially, rounded abaxially, 5–23 cm long, 1–2 cm diam.; geniculum 1.6–2 cm long; blades obovate to oblanceolate, moderately thick, acuminate at apex, attenuate, sometimes cuneate (rarely rounded or subcordate) at base, (32) 40–180 cm long, (9)13–50 cm wide; both surfaces semiglossy; the midrib acutely raised above and below; primary lateral veins 9–14 per side, raised above and below; lesser veins less conspicuous. INFLORESCENCE usually pendent, shorter than leaves; peduncle 16–80 cm long; spathe lanceolate-linear, moderately thin, purple or green sometimes tinged purple, 4–45(50) cm long, 1–5 cm wide; gradually cuspidate-acuminate at apex, rounded to truncate at base; spadix dull green soon tinged throughout with lavender (B & K Purple 6/5), 6–34(47) cm long, 0.6–1.5 cm diam. at base, 2–7 mm diam. at apex; flowers rhombic, 2.4–2.5 mm in both directions, the sides straight to sigmoid; 6–7 flowers visible in the principal spiral, 8–12 flowers visible in the alternate spiral; tepals matte, lateral tepals 1.2–1.3 mm wide, the inner margins broadly rounded; pistils green, emergent but not raised; stigma linear, ca. 0.9 mm long; stamens emerging in a slow progression from the base; anthers pale yellow, held at edge of tepals and laying over pistil; thecae ellipsoid; pollen pale yellow-orange, fading to white. INFRUCTESCENCE with spadix to 60 cm long; berries red, oblong-elliptic, rounded at apex, 1–1.5 cm long; seeds 2, oblong, flattened, 3.3 mm long. Figs. 166 and 167.

The species occurs in western Mexico (Chiapas) along the Pacific slope of Guatemala and along both the Atlantic and Pacific slopes from Nicaragua to Panama. There is also a single collection from Honduras (Atlantic slope) that appears to be this species. The species also occurs in Colombia and has been collected in Chigorodó and Dabeiba in Antioquia. *Anthurium salviniae* occurs from near sea level to 1,400 m, in wetter parts of tropical moist forest, in premontane wet, tropical wet, and also, rarely, in premontane rain forest.

Anthurium salviniae has long been called *A. tetragonum* but that name is a synonym of *A. schlechtendalii,* a species ranging from Mexico to Honduras or Nicaragua on the Atlantic slope. Although leaves of the two species are very similar, *A. salviniae* is a member of section *Pachyneurium* and can be distinguished by its long-tapered, pale lavender spadix, long-tapered

FIGURES 168–171. 168. *Anthurium salvadorense* Croat, *Croat 42092*.—169. *Anthurium scandens* (Aubl.) Engl., *Croat XX-6*.—170. *Anthurium scandens* ssp. *pusillum* Sheffer, *Selby 77-2828*.—171. *Anthurium scherzerianum* Schott, *Croat 35583*.

spreading spathe, and fist-shaped, cucullate cataphylls. In addition the leaves of *A. salviniae* usually dry darker and thinner. *Anthurium schlechtendalii* usually has a shorter, blunter spadix and a short, thick spathe that is usually reflexed and often twisted. The spadix is darker violet-purple and is not at all glaucous at anthesis.

A collection in cultivation at Missouri Botanical Garden from the Río Maje region of Panama in Panamá Province is unusual in having dark violet-purple rather than red berries.

COSTA RICA. ALAJUELA: N of Bijagua, *Croat 36480* (MO); NW of Zarcero, *Croat 43640* (MO). CARTAGO: SE of Platanillo, *Croat 36808* (MO); NE of Tapantí, *Lent 1034* (GH). GUANACASTE: vicinity of Tilarán, *Standley & Valerio 44445* (US). PUNTARENAS: vicinity San Vito de Java, *Croat 32898* (MO).

GUATEMALA. ESCUINTLA: between Escuintla and Santa Lucía Cotz, *Standley 63469* (F). RETALHULE: region of Ajaxá, *Standley 88227* (F); W of Retalhule, *Standley 87499, 88391* (F). SAN MARCOS: La Trinidad, *Croat 40902, 40903* (MO). SANTA ROSA: near Cuilapilla, *Standley 78060* (F); Naranjo, *Hyde & Lux 4278* (NY, US). SACATEPEQUEZ: near Las Lajas, *Standley 58294* (F). SUCHITEPEQUEZ: E of Mazatenango, *Croat 32786* (MO).

HONDURAS. ATLÁNTIDA: Lancetilla Valley near Tela, *Standley 53228* (US).

MEXICO. CHIAPAS: Escuintla, *Croat 43845, 43877* (MO); *Matuda s.n., 18630* (MEXU); *Matuda 16377* (F, MEXU, MO); *Matuda 16776* (F, MEXU); *Matuda 18043* (MEXU, UCLA); *Matuda 18381* (DS, MEXU); *Matuda 18519* (DS, MEXU, UCLA); between Finca California and summit of Monte Ovando, *Croat 47572, 47573* (MO); Guatimoc, *Miranda 1763* (MEXU).

NICARAGUA. RÍO SAN JUAN: San Juan del Norte (Greytown), *Smith 87* (MO). ZELAYA: S slope of Cerro El Inocente, *Stevens 6793* (MO).

Anthurium scandens (Aubl.) Engl., Mart. Fl. Bras. III. 2: 78. 1878.

a. **Anthurium scandens** ssp. **scandens.** *Dracontium scandens* Aubl., Hist. Pl. Guiana Franc. 2: 836. 1775. TYPE: French Guiana. (Drawing by Plumier in Amer. Nascentium Icon. tab. 74. 1703. BM, P.)

Pothos violacea Swartz, Prodr. 32. 1788. TYPE: Jamaica, *Swartz s.n.* (not seen).

Dracontium repens Descourt., Fl. Antill. 7: t. 499. 1829. TYPE: (Plate 499 serves as the type.)

Anthurium violaceum (Swartz) Schott, Melet. 22. 1832. TYPE: *Swartz s.n.* (not seen).

Anthurium violaceum forma *latifolia* Kunth, Enum. Pl. 3: 68. 1841. TYPE: (not seen).

Anthurium violaceum forma *angustifolia* Kunth, Enum. Pl. 3: 68. 1841. TYPE: (not seen).

Anthurium leucocarpum Schott, Oesterr. Bot. Wochenbl. 7: 53. 1857. TYPE: Mexico. *Schiede* (Not seen.) (Photos of Schott Aroid Drawing #279, NYGB Neg. #N.S. 3804 and Schott Aroid Drawing #282, NYBG Neg. #N.S. 3805.)

Anthurium dolosum Schott, Oesterr. Bot. Z. 8: 179. 1858. TYPE: Guatemala. Near San Pedro and San Lucia, *Wendland 273* (GOET, hololectotype; K, isolectotype; here designated).

Anthurium rigidulum Schott, Oesterr. Bot. Z. 8: 180. 1858. TYPE: Costa Rica. San José, *Hoffmann 508* (Photo of Schott Aroid Drawing #270, NYBG Neg. #N.S. 3807).

Anthurium virgosum Schott, Oesterr. Bot. Z. 9: 100. 1859. TYPE: Brazil. Río de Janeiro, *Riedel* (K).

Epiphytic creeper; stems usually less than 1 m long; roots numerous along stem, ca. 3 mm diam., gray-green; cataphylls 3–6 cm long, drying brown, weathering to reticulate fibers and persisting around stem. LEAVES spreading; petioles sharply sulcate, rounded abaxially, 2–8.5 cm long, 2–3 mm diam.; geniculum 2–3 mm long, nearly obscure; blades ovate-elliptic to lanceolate-elliptic, moderately thick, (3.5)6–13 cm long, (1.5)2–5 cm wide, short-acuminate at apex, acute to rounded at base; upper surface semiglossy, lower surface conspicuously brown punctate; the midrib acutely raised above, diminished and sunken in apical half of blade, convexly raised below; primary lateral veins 3–10 per side (sometimes more), departing midrib at 35°–40° angle, weakly sunken above, ± obscure above and below; collective vein arising from the base, extending straight to apex, 3–5 mm from the margin. INFLORESCENCE erect to pendent, shorter than leaves; peduncle 1.5–6.5 cm long, 1–1.3 mm diam., equalling or longer than petioles; spathe pale green, ovate to narrowly ovate, 8–16 mm long, ca. 4 mm wide, reflexed at anthesis, abruptly acuminate at apex; spadix yellow-green, sometimes becoming lavender, 1.3–2 cm long, 2–3 mm diam. midway; flowers rhombic, 2–4 mm in both directions, the sides straight to sigmoid; 2–3 flowers visible in either spiral; tepals semiglossy, lateral tepals ca. 1.2 mm wide, the inner margin weakly concave to ± straight; pistil greenish-white, scarcely emergent; stigma brushlike, exserted, ca. 0.2 mm long; stamens emerging in a prompt and complete sequence from the base, held at edge of tepals and inclined over pistil; anthers white; thecae ovate, somewhat divaricate; pollen white. INFRUCTESCENCE spreading, the spathe persisting; spadix 2.5–3.5 cm long, to 7 mm diam.; berries usually pale violet to almost white, sometimes purple, obovoid, rounded at apex, 5–8 mm wide; seeds 1 or 2 per locule, pale yellow, ovoid, ca. 2 mm long, 1 mm wide. Fig. 169.

Anthurium scandens is known from southern Mexico and the West Indies to southern Brazil, ranging from sea level to 2,700 m. This is the most widespread aroid in the New World and, doubtless, the most ecologically diverse as well, occurring in tropical moist, premontane wet, tropical wet, premontane rain, and lower montane rain forest life zones.

The species is a member of section *Tetraspermium* and is distinguished by its more or less scandent habit, elongate internodes with usually persistent cataphylls, usually oblong-elliptic, glandular-punctate blades, reflexed green, more or less ovate spathe, cylindroid, usually pale green spadix, and pale lavender to almost white berries.

According to Sheffer et al. (1980), the great variability in the species is due at least in part to the fact that it represents a polyploid complex containing diploids, tetraploids, and heptaploids. The cytology of the group is insufficiently known, so it is not certain whether the different ploidy levels are correlated with morphological variation.

The species is closely related to *A. trinerve*, with which it has long been confused. The differences separating the two species are outlined in the key. *Anthurium scandens* is most easily distinguished by its spathe, which is reflexed at anthesis, whereas the spathe of *A. trinerve* is persistently erect even after anthesis.

BELIZE. CAYO DISTRICT: no other location, *Lundell 6255* (MICH); vicinity of Cuevas, S of Millionario, *Croat 23592* (MO); Roaring Creek, *Dwyer 12690* (MO). STANN CREEK DISTRICT: Stann Creek Railroad, *Schipp 78* (MICH, MO, UC); N of Victoria Peak, *Gentry 7912* (MO). TOLEDO DISTRICT: W of Columbia Forest Station, *Croat 24309* (MO, DAV); *Dwyer 9946* (MO).

COSTA RICA. No other location, *Brade 2518* (BR). ALAJUELA: Laguna de A. Ruiz, *Rodrigues 264, 280* (UC); NW of Cariblanco, *Luteyn 3216* (MO); W of Fortuna, *Taylor 11711* (MO); NW of Zarcero, *Croat 43530* (MO); *Smith 230* (MO). CARTAGO: no other location, *Brade 2506* (BR); E of Cachí, *Croat 47082, 47083* (MO); Cartago, *Brade 2500* (BR); SE of Cartago, *Harmon & Fuentes 6315* (MO, UMO); La Carpintera, *Allen 514* (MO); *Brade 2515* (BR); near Las Cancavas, *Hunnewell 16564* (WIS); between Moravia and Quebrada Platanillo, *Croat 36632* (MO); Peralta, *Stork 494* (UC); Tapantí, *Tissene 1284* (WIS); Trinidad, *Luteyn & Wilbur 4484* (DUKE, MO); SE of Trinidad, *Wilbur & Luteyn 18682* (DUKE); W of Turrialba, *Croat 36846* (MO); Volcán Irazú, *Moore 6670* (BH). GUANACASTE: Aguas Calientes, *Pittier 1160* (BR); La Lagunilla, *Pittier 10473* (BR); NW edge of Lake Arenal, *Croat 1033* (MO); La Palma, *Greenman & Greenman 5446* (MO). HEREDIA: S of San Miguel, *Lent 36* (DAV); Vara Blanca, *Skutch 3665* (MICH, MO); Volcán Barba, *Brade 2509* (BR). LIMÓN: Hacienda Tapezco-Hda. La Suerte, W of Tortuguero, *Davidson 6935* (MO); vicinity USDA Rubber Experimental Station, Talamanca, *Pittier & Tonduz 9227, 9235* (BR); *Tonduz 9511* (BR). PUNTARENAS: Las Cruces Botanical Garden, *Peterson J-2243* (BH); Osa Peninsula, W of park headquarters at Sirena, *Liesner 2906* (MO); Rincón de Osa, *Liesner 1701, 1804, 1997* (MO); N of San Vito, *Davidson 7153* (MO); *Stevens 232* (MO); SAN JOSÉ: without further locality, *Brade 2501* (BR); *Pittier 2445* (BR); at Cascajal, *Utley 5237* (DUKE); *Lent 2090* (MO); N of Hwy. 12, *Croat 43386* (MO); between Río Paquita and Río Viejo, *Dodge & Goerger 9826* (MO); N of San Isidro del General, *Harmon & Fuentes 6229* (MO, UMO); between San Isidro del General and Dominical, *Croat 35333* (MO); vicinity San José, *Pittier 1240* (BR); *Tonduz 1255* (BR); Santa María de Dota, *Pittier 2488* (BR); lower eastern slopes of Volcán Barba, *Luteyn 3575* (MO); beyond end of Calle Yerbabuena, *Luteyn 3369* (MO). SAN JOSÉ & CARTAGO: SE of Casa Mata, *Utley 4743* (DUKE).

EL SALVADOR. SANTA ANA: Finca La Cumbre, *Montalvo 3252* (MO); *Weberling & Lagos 1086* (GOET).

GUATEMALA. ALTA VERAPAZ: Cobán, *Tuerckheim 1355* (MO), *1923* (BR, MO); vicinity Cubilhuitz, *Steyermark 44357* (MO); road to El Estor, *Croat 41489* (MO); near Tucurú, *Standley 70725* (MO). BAJA VERAPAZ: along hwy. ca. 14 mi to Cobán, about 1 mi S of turnoff to Salamá, *Croat 41146* (MO). HUEHUETENANGO: between Maxbal and Xoxlac, *Steyermark 48978* (MO). PETÉN: El Rosario, *Harmon & Fuentes 5780* (UMO); Santa Teresa, *Lundell 2671* (MICH); Tikal National Park, *Lundell 16671* (DS); Tikal, *Contreras 1128* (DAV); *Harmon & Fuentes 5833* (UMO). SACATEPEQUEZ: SW of Alotenango, *Croat 42029* (MO). SAN MARCOS: Finca El Porvenir, *Steyermark 37542* (MO). SUCHITEPEQUEZ: near Mazatenango, *Bernoulli 388* (BR). ZACAPA: along Rillito from Volcán de Monos, *Steyermark 42342* (MO).

HONDURAS. ATLÁNTIDA: above Lancetilla, *Yuncker 4557* (MICH). COMAYAGUA: Jardines, *Barkley & Smith 40875* (MO); near El Achiote, *Yuncker et al. 5980* (MO). COPÁN: W of Copán, *Croat 42519* (MO); Forest Monte Grueso, *Cuellar & Hernandez 5181* (MO). CORTÉS: N of Lake Yojoa, *Croat 42727, 42738* (MO); Lake Yojoa, *Yuncker 4836, 4880* (MICH, MO). EL PARAÍSO: trail, Danlí to Finca La Emilia, *Carlson 2563* (MICH). MORAZÁN: Hoya Grande, *Williams & Molina 10037* (MO); between Tegucigalpa and El Zamorano, *Clewell 3664* (MO).

MEXICO. CHIAPAS: Munic. of Berriozábal, *Breedlove 20286* (MICH, MO); *Miranda 6723* (MEXU); *Moore & Brossard 6327* (BH); Cerro Baúl, *Croat 47669* (MO); SW of Comitán, *Carlson 1820* (MICH); vicinity Comitán, *Miranda 2697* (MEXU); between Ixtapa and Pichucalco, *Croat 47837* (MO); Lake Montebello, *Croat 46658* (MO); Monte Ovando, *Matuda 2097, 4205* (MEXU, MICH); *Matuda 17911* (MEXU); Ocozocoautla de Espinosa, *Carlson 2103* (MICH); *Rzedowski 614* (MEXU); S of Palenque, *Thorne & Lathrop 40565* (RSA); Munic. Pichucalco, *Gilly & Hernandez 113* (MICH); Munic. Pueblo Nuevo Solistahuacán, *Kennedy et al. 1443* (MO); San Juan Panama, *Matuda 18175* (MEXU); Siltepec, *Matuda 18301* (MEXU); between Tapachula and Unión Juárez, *Croat 47207* (MO); ruins of Bonampak, *Hoover 192, 208* (MO). JALISCO:

Autlán, *McVaugh 10219* (MEXU, MICH); *Wilbur & Wilbur 1738* (MICH). OAXACA: between Teotitlán del Camino and Santa María Chilchotla, *Croat 48323, 48385* (MO); between Tuxtepec and Oaxaca, *Croat 47983* (MO). PUEBLA: Hueytamalco, *Conrad 88, 152* (MEXU); Teziutlán, *Gold 253* (MEXU). TABASCO: *Sheffer 225, 226* (UH); Teapa, *Birdsey 235* (UC); *Conrad 2873* (MO); *Gilly & Hernandez 213* (MEXU, MICH). VERACRUZ: *Schnee V* (MEXU); Rancho la Laguna, *Chazaro 771* (JAL); near Pedre al Rumbo, *Lot et al. 1815* (MEXU); Coatepec, *Dorantes 1800* (MICH, MO); *Ventura 10382* (MEXU, UMO); *Zola & Baker 98* (XAL); Atoyac, *Matuda 1411* (MEXU, MICH, MO); Lake Catemaco, *Gonzales 856* (MEXU, MICH); *Sousa 19* (MEXU); E of Córdoba, *Lundell & Lundell 12532* (MICH); *Matuda S-150* (MICH); *Matuda 838* (MEXU, MICH); between Córdoba & Fortín, *Miranda 620, 4836* (MEXU); Córdoba, *Rowell et al. 17M663* (MEXU); *Rzedowski 18895* (MEXU, MICH); Coyame, *Beaman 5296* (MEXU); El Mirador, E of Huatusco, *Croat 44011* (MO); vicinity of Huatusco, *Moore & Bunting 8854* (BH); vicinity of Mirador, *Ventura 5421* (MICH); Fortín, *Kerber 293* (MICH); *Kerber 294* (BR); *Lot 537* (XAL); Hidalgotitlán, *Dorantes 3002* (XAL); *Dorantes 3088* (MEXU); *Valdivia 113, 225, 439, 952, 1048, 1404, 1567, 1615* (MEXU, MO); *382* (XAL); *1127, 1680* (MO); *1217* (MEXU); *Valdivia & Matuda 517* (XAL, MO); *1099* (XAL); Jalapa, *Barkley et al. 2600* (MEXU, MICH); *Boege 2058* (MEXU); *Dorantes 124* (BR, MO, XAL); *Sousa 4844* (MEXU); Jesús Carranza, *Vazquez 703* (XAL); Misantla, *Ventura 7153* (DS, MICH, MO); Ocotal Grande, *Beaman 5451* (MEXU); Orizaba, *Moore 6211* (BH, UC); Pedregal, *Yanez 538* (F); San Andrés Tuxtla, *Kennedy & Howitz 3677* (MICH, MO); *Trigos 88* (MEXU); *160* (XAL) vicinity Santiago Tuxtla, *Beaman 6411* (F, XAL); *Sousa 2419* (MEXU); vicinity Barra de Sontecomapan, *Beutelspacher s.n.* 15/3/69 (MEXU); *Hernandez y Trigos s.n.* (MEXU); vic. Tlapacoyan, *Goméz-Pompa & Nevling 1144* (XAL); Zomajapa, *Valdivia 2112* (XAL); Yecuatla, *Goméz-Pompa & Riba 161* (MEXU); *Goméz-Pompa 1838* (MEXU); vicinity Zacualpan, *Galeotti 6052* (BR); *Purpus 5764* (UC, MO); Zongolica, *Santos 3680* (MICH); *Valdivia 2141* (XAL).

NICARAGUA. GRANADA: Finca Cutirre, *Atwood AN64* (MO); Volcán Mombacho above Finca Las Delicias, *Atwood A50* (MO); SE flank of Mombacho, *Neill N30, N56* (MO); *Stevens 4365* (MO); *Croat 39116* (MO). JINOTEGA: Cerro Zamaria, *Atwood AN118* (MO); NW side of Lake Abanas, *Croat 42989* (MO); vicinity El Crucero, *Stevens 3500* (MO); between La Danta and La Luna, *Stevens 9630* (MO). MATAGALPA: vicinity Matagalpa, *Williams & Molina 42548* (MICH); vicinity Sébaco, *Webster et al. 12506* (DAV); Tuma Village, *Atwood A69* (MO). NUEVO SEGOVIA: N of San Fernando, *Stevens 3300* (MO). ZELAYA: Caño Zamora, *Stevens 8826* (MO); trail from Cerro El Inocente to Cerro Saslaya, *Stevens 6696* (MO); vicinity Waní, *Stevens 7341* (MO).

b. **Anthurium scandens ssp. pusillum** Sheffer, Aroideana 3(3): 86. 1980. TYPE: Costa Rica. Cartago: Southeast of Tapantí, Río Grande de Orosi, 1,400 m, 16 April 1967, *R. W. Lent 830* (F, holotype).

Anthurium scandens ssp. *pusillum* occurs from Honduras to Colombia and Venezuela at elevations of 600 to 2,500 m in lower montane moist, premontane wet, lower montane rain, and premontane rain forest life zones.

The subspecies *pusillum* differs from the typical subspecies in usually having a much smaller spadix (usually with fewer than 13 flowers), usually 2–10 mm long. Sheffer (1974) believes that the subspecies may represent one of the diploids upon which the polyploid complex has been built. Fig. 170.

COSTA RICA. CARTAGO: E of Cachí, *Croat 47062* (MO); Carpintera, *Stork 1143* (MICH); S of Muñeco, *Luteyn 3880* (DUKE, MO); Tapantí, *Croat 47048* (MO). SAN JOSÉ: along CR 220, *Luteyn 3593* (DUKE); San Josecito, *Primack & Luteyn 353* (DUKE).

NICARAGUA. JINOTEGA: vicinity Aranjuez, *Stevens 5606, 5936* (MO). ZELAYA: trail from Cerro El Inocente to Cerro Saslaya, *Stevens 6695* (MO).

Anthurium scherzerianum Schott, Oesterr. Bot. Wochenbl. 7: 53. 1857. TYPE: Guatemala, *Scherzer s.n.* (B, holotype (2 sheets); BP, isotype).

Epiphytic or terrestrial; stems very short, roots numerous, thin; cataphylls thick, to 1.5 cm long, caudate at apex, drying brown, persisting as fibers. LEAVES spreading; petioles terete, 4–20 cm long, 1–3 mm diam.; geniculum 4–7 mm long; blades moderately thick, linear to elliptic or lanceolate, 5–26 cm long, 1.5–6.5 cm wide, narrowly acuminate at apex, obtuse to cuneate at base; upper surface semiglossy, the lower surface matte, both surfaces densely punctate; the midrib acutely raised above, sunken at apex; prominulous below; primary lateral veins 8–11 per side, departing midrib at 45° angle, nearly obscure above and below, loop-connecting to collective vein, lesser veins obscure; collective vein arising from near the base or one of the lowermost primary lateral veins, 1–3 mm from the margin. INFLORESCENCE erect, equalling or longer than leaves; the peduncle 14–52 cm long, ca. 2 mm diam.; spathe moderately thick, bright red-orange (B & K Red 7/2.5), elliptic to ovate, 3.7–12 cm long, 2.4–6 cm wide, abruptly short-acuminate at apex, cordate at base (the lobes sometimes overlapping); spadix pale orange to red, 2–8 cm long, ca. 4 mm diam. midway, tapered at apex and usually coiled; flowers square, 2 mm in both directions, the sides straight to ± sigmoid, 2–3 flowers visible in the principal spiral, 5–6 flowers visible in the alternate spiral;

tepals glossy, sparsely and minutely papillate, lateral tepals ca. 1.3 mm long; pistil weakly emergent, somewhat translucent; stigma linear, 0.4–0.6 mm long; stamens emerging from base, the first lateral preceding second by 2–3 spirals, the laterals emerged well above midway before alternates emerge, exserted on flattened, short filaments, ca. 3 mm long, 0.5 mm wide; anthers white, held at edge of tepals, ca. 0.3 mm long, 0.5–0.7 mm wide; thecae ellipsoid, slightly divaricate; pollen white. INFRUCTESCENCE with orange to red berries. Fig. 171.

The species is found in Costa Rica at elevations of 1,300 to 2,100 m in premontane rain, lower montane rain, and montane rain forest life zones on the Atlantic slope of the Cordillera Central and the Cordillera de Talamanca. It has been collected most commonly in the Tapantí and La Hondura areas.

Anthurium scherzerianum is a member of section *Porphyrochitonium* and is easily recognized by the large, showy, bright orange or red-orange to red spathe, and coiled spadix. The species is now commonly cultivated throughout the world and about 40 different forms are recognized in cultivation. The species has no close relatives.

The type of *A. scherzerianum* was believed to have been collected in Guatemala; however since that time no other collections have been seen from that country. So far the species has been found only in Costa Rica, where it is plentiful, and it is likely that the type was collected there.

COSTA RICA. ALAJUELA: edge of Lake Hule, *Luteyn 3221, 3351* (DUKE). CARTAGO: no other location, *Burger & Stolze 5621* (NY, WIS); S of Cartago, *Maxon 503* (NY); *Stork 1913, 4534* (UC); Navarro Valley, *Stork 1701* (MICH); between Quebrada Honda and Río Sombrero, *Luteyn 3232* (DUKE, MO); SE of Orosi, *Lellinger & White 1486* (MO); below Palo Verde, *Luteyn 3339* (DUKE, MO); Río Sombrero, *Luteyn et al. 4528* (DUKE); Tapantí, *Croat 36077* (MO); *Lent 836* (NY); *Taylor 4468* (MO, NY); *Tessene 1296* (WIS); Turrialba, *Brade 2504* (BR). HEREDIA: S of Cariblanco, *Croat 35800* (MO); N of Vara Blanca, *Croat 35583* (MO). SAN JOSÉ: Santa María de Dota, *Stork 1883* (MICH, UC); Tablazo, *Pittier 7909* (BR).

Anthurium schlechtendalii Kunth, Enum. Pl. 3: 75. 1841.

a. **Anthurium schlechtendalii** ssp. **schlechtendalii.** TYPE: Mexico. Hacienda de la Laguna, *Schiede & Deppe* (not seen).

Anthurium mexicanum Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1: 21. 1849. TYPE: Mexico. Veracruz: between Colipa & Misantla (not seen).

Anthurium kunthianum Liebm., Ann. Sci. Nat. Bot., Ser. IV, 2: 372. 1854. TYPE: Mexico (no type cited).

Anthurium brachygonatum Schott, Prod. Aroid. 468. 1860. TYPE: Mexico. Veracruz: Cordoba, *Kerber s.n.* (B) (see discussion).

Anthurium tetragonum Hook. ex Schott, Prod. Aroid. 475. 1860. TYPE: Locality unknown (not seen).

Anthurium fortinense Engl., Bot. Jahrb. Syst. 25: 366. 1898. TYPE: Mexico. Veracruz: Fortin, *Kerber 9b* (B).

Anthurium tikalense C. Lundell, Wrightia 3: 161, Fig. 55. 1966. TYPE: Guatemala. Petén: Tikal National Park, on temple in Group "H," March 1, 1961, *C. L. Lundell 18198* (LL).

Usually epiphytic, sometimes epipetric; stem usually short, 2.5–5.5 cm diam.; internodes and leaf scars hidden by dense mass of thick, greenish roots, 3–8 mm diam.; cataphylls moderately thick, 7.5–16 cm long, caudate-apiculate at apex, drying brown, persisting as reticulate fibers. LEAVES erect; petioles 12–23 cm long, 0.5–2 cm wide, trapezoidal, the abaxial margins sometimes sharply to obtusely ribbed, widest adaxially, shallowly sulcate; geniculum 1–2 cm long; blades obovate-elliptic, thick, acute to short-acuminate at apex, acute to obtuse at base, 30–112 cm long, 10–58 cm wide; broadest near or above middle; both surfaces matte to semiglossy; midrib flat to weakly rounded at base above, becoming more acute sometimes weakly ribbed, diminished and sunken at apex, raised and square at base below, rounded at apex; primary lateral veins 15–16 per side, raised on both surfaces, departing midrib at 50° angle, straight nearly to margin, then arching toward apex, lesser veins scarcely visible; collective vein arising from primary lateral vein in apical one quarter of blade, 2–5 mm from margin, sunken above, raised below. INFLORESCENCE spreading, shorter than leaves; peduncle 33–43 cm long, 6–11 mm diam., terete to weakly flattened and ribbed; spathe coriaceous, green heavily tinged with violet-purple, linear-lanceolate to lanceolate, 15–28 cm long, 1.5–5 cm wide, acuminate at apex, obtuse at base, strongly reflexed, inserted at 70° angle on peduncle; spadix green, 8–29 cm long, 1.7–2 cm diam. at base, 4–6 mm diam. at apex; flowers square, 2.2–2.6 mm in both directions, the sides straight to weakly sigmoid; 7–17 flowers visible in the principal spiral, 10–14 flowers visible in the alternate spiral; tepals green, matte, with purple punctations, the outer margins purplish, lateral tepals 1.1–1.3 mm wide, the inner margins convex, turned up against pistils; pistils emergent

to 1 mm, dark purple; stigma linear, 0.8 mm long, with minute droplet ca. 4 days before stamens emerge, dry, black as stamens emerge; stamens emerging rapidly from the base, lateral stamens emerging to midway before alternate stamens emerge, exserted on translucent filaments, ca. 0.5 mm long, 1 mm wide, which retract to hold anthers at side and inclined over pistil; anthers pale orange, 0.9 mm in both directions; thecae ± oblong, scarcely divaricate; pollen pale orange fading to cream. INFRUCTESCENCE arching-pendent; spathe brown, persistent; spadix up to 65 cm long, 5 cm diam.; berries bright red, lanceolate-elliptic 1–1.5 cm long; pericarp thick; mesocarp pulpy, white, with numerous raphide cells; seeds 2, greenish-white, 5.5–6 mm long, ca. 1.5 mm wide. Figs. 172 and 173.

Anthurium schlechtendalii is in section *Pachyneurium* and consists of two subspecies. The subspecies *schlechtendalii* ranges from Mexico (central Veracruz) to Nicaragua on the Atlantic slope at an elevational range from near sea level to 1,600 m (most commonly below 1,000 m).

This species is most closely related to *A. schlechtendalii* ssp. *jimenezii* from the Pacific slope of Mexico, which differs by occurring in seasonally drier habitats, by its generally smaller leaves, and by its frequently narrowly ovate, usually erect spathe.

Anthurium schlechtendalii merges into the range of *A. salviniae* only in a few areas in the mountains of southeastern Chiapas, such as on Monte Ovando, where both species were seen growing. Specimens collected in the municipios of Siltepec, Escuintla, and Acacoyagua tend to have leaf blades approaching the texture of those of *A. salviniae* but have the inflorescences and cataphylls of typical *A. schlechtendalii*. See discussion following *A. salviniae* for separation characters for these two taxa.

In discussing Mexican aroids, Bunting (1965) included an illustration of a plant cultivated at Cornell University and reputedly collected by H. Moore in Mexico. This is almost certainly *A. crenatum* (L.) Kunth from the West Indies and perhaps represents a mixing of labels in the greenhouse. Two vouchers presumably prepared from this plant (*Bunting 1579* and *Nicolson 603*) tend to confirm this. *Anthurium crenatum* so far as is known is restricted to Puerto Rico and the Virgin Islands.

Studies of populations of *A. schlechtendalii* in Mexico and elsewhere show most morphological characters to be variable. Petiole shape, although usually trapezoidal in cross-section with the angles moderately acute, may be broadly rounded abaxially, such as those illustrated by Schott for *A. brachygonatum* [see Schott drawing No. 473 (W)]. Although Bunting (1965) considered this distinct from *A. schlechtendalii*, it is believed to be a form of an unusually variable species.

BELIZE. No other location, *Schipp S-402* (MICH, MO, NY, UC) BELIZE: Northern River, *Gentle 1291* (F); no other location, *Bartlett 11325* (MICH); Gracy Rock, *Croat 23851, 23896* (MO); *Liesner & Dwyer 1472* (MO). CAYO DISTRICT: no other location, *Chanek 53* (MICH, MO); W of Hummingbird Highway, *Spellman & Newey 1984* (MO); vicinity La Flor, S of Grano de Oro, *Croat 23811* (MO); Waterhole camp near Vaca, *Gentle 2567* (MICH). COROZAL DISTRICT: no other location, *Gentle 597* (MICH). ORANGE WALK DISTRICT: Indian Church, *Arnason & Lambert 17186* (MO). TOLEDO DISTRICT: S of Mayan Village of San José, *Croat 24297, 24333, 24431* (MO); *Vanderveen 658* (MO); Moffredge Lagoon, *Gentle 5372* (TEX); Río Grande, *Gentle 4723* (TEX).

GUATEMALA. ALTA VERAPAZ: La Tinta, *Smith 1530a* (US); W of Teleman, *Croat 41536, 41551* (MO); between Tucurú and El Estor, *Croat 41525, 41529* (MO). ESCUINTLA: SW of Palín, *Harmon 2420* (UMO). HUEHUETENANGO: between Ixcán & Finca San Rafael, *Steyermark 49411* (F); below La Libertad, *Steyermark 51171* (MO). IZABAL: E of El Estor, *Jones & Facey 3456* (NY, TEX); vicinity Lago Izabal, *Jones & Facey 3437* (NY, TEX); S of Modesto Mendez, *Harmon & Fuentes 2115* (MO, UMO); S of Puerto Barrios, *Croat 41802, 41839* (MO); vicinity Quiriguá Viejo, *Standley 24053* (NY, US); between Virginia and Lake Izabal, *Steyermark 38769* (F). PETÉN: Dolores, *Contreras 2254* (LL); El Paso, *Herman 14664, 14671* (MICH); *Lundell 1573* (MICH); La Libertad, *Lundell 2873* (MICH); Macanché Lake, *Contreras 920* (LL); Santa Teresa, *Lundell 2708* (MICH); *2889* (MICH, NY); Tikal, *Bernhardt T6* (MO); *Contreras 1618* (LL); *Croat 24753* (MO); *Lundell 15410* (TEX); Uaxactún, *Bartlett 12295, 12296* (MICH). SAN MARCOS: Volcán Tajumulco, *Steyermark 37078* (F).

HONDURAS. COPÁN: E of Copán, *Croat 42508, 42521* (MO). CORTÉS: SW of Omoa, *Croat 42564* (MO); vicinity La Pimienta, *Molina 5623* (F); S of Porterillos, *Croat 42706* (MO); W of Puerto Cortés, *Nelson et al. 2904* (MO). SANTA BÁRBARA: NW side of Lake Yojoa, *Croat 42757* (MO). YORO: vicinity Coyoles, *Yuncker et al. 8132* (MO, NY, US); *8174* (F, MO).

MEXICO. CHIAPAS: Acacoyagua, *Matuda 19646* (DS); Angel Albino Corzo, *Ton 3880* (MAD, DS); vicinity Bochil, *Roe et al. 1132* (WIS); *Ton 2587* (DS); vicinity Chiapa de Corzo, *Breedlove 26872* (DS); *Croat 46437* (MO); *Miranda 2646* (MEXU); SW of El Jocote, *Croat 40706* (MO); Escuintla, *Croat 43879* (MO); *Matuda 17973, 19645* (MEXU); between Huixtla and Motozintla, *Breedlove 28609* (DS); *Croat 40766, 47225* (MO); Ixtapa, *Laughlin 723* (DS, MICH, NY); *1599* (DS, MEXU, TEX); vicinity Jitotol, *Thorne & Lathrop 41341* (DS); vicinity Las Margaritas, *Breedlove 33199, 33446* (DS); vicinity Siltepec, *Croat 47250* (MO); *Ma-*

FIGURES 172–175. 172. *Anthurium schlechtendalii* Kunth, *Croat 40068*.—173. *Anthurium schlechtendalii* Kunth, *Croat 43879*.—174–175. *Anthurium schottianum* Croat & Baker, *Croat 43247*.

tuda 18798 (MEXU); Ocosingo, ruins of Yaxchilan, *Breedlove 33872* (DS); between Palenque and Ocosingo, *Croat 40319* (MO); Ocozocoautla de Espinosa, *Breedlove & Smith 21982* (DS, MO); *Breedlove 29004, 30358, 36555, 38332* (DS); *Croat 40587, 40626, 40653* (MO); *MacDougall H261* (NY); vicinity Palenque, *Croat 40215* (MO); *Hoover 282* (MO); Pichucalco, *Breedlove 35048* (DS); *Croat 40074, 40086* (MO); *Gilly & Hernandez 182* (MICH); vicinity Pueblo Nuevo Solistahuacán, *Breedlove 26042* (DS); *Roe et al. 1239* (US); Raudales Mal Paso, *Quintero 3441* (MEXU); Tenejapa, *Breedlove 6242* (DS, F, MICH); *11731* (F, MICH, TEX); *Ton 350* (DS); Tuxtla Gutiérrez, *Guzmán 13* (MEXU). GUERRERO: Minas, *Hinton 10125* (GH). NAYARIT: vicinity Tepic and Jalcocotán, *Croat 45337* (MO); *Dressler 339* (MO); *Gentry et al. 10734* (MO). OAXACA: no other location, *Calderón 145* (GH); Cerro Concordia, *Morton & Makrinius 2731* (F, US); Chinantla, *Ramirez 144* (MEXU); Matatengo Gorge (Cultivated at MO), *Croat 32712, 32717* (MO); Santo Domingo Tehuantepec, *Williams 70, 83* (MICH); Temascal, *Sousa 936, 1037, 1801* (MEXU); S of Teotitlán del Camino, *Croat 48296, 48374* (MO); vicinity Tuxtepec, *Calderón 844* (MICH); *Conrad & Conrad 3251* (MO); *Miranda 4274* (MEXU); *Moore & Bunting 8907* (BH); *Quintero 1820* (MEXU); *Rzedowski 25480, 25483* (US); *Sousa 1809, 1825* (MEXU); *Webster & Breckon 15400* (DAV); S of Valle Nacional, *Croat 39707, 39708, 39738, 39756* (MO). TABASCO: Balancán, *Valdivia 2028, 2052* (XAL); NW of Cardenas, *Barlow 26/10* (WIS); E of Teapa, *Croat 40109, 47894* (MO); S of Villahermosa, *Conrad et al. 2866* (MO); *Croat 40068* (MO). VERACRUZ: Laivaparu, *Purpus 1400* (MICH); Actopan, *Ortega-Ortiz 563* (F, XAL); Atoyac, *Rosas 1126* (F, XAL); Barra Platanar, *Dorantes et al. 1287* (MEXU); Catemaco, *Sousa & Sousa 14* (MEXU); on road to Jalapa, *Dorantes 505* (CAS, F, MEXU); Coatepec, *Castillo & Dillon 483, 715* (MO); Cordillera, *Galeotti 6055* (BR); Córdoba, *Miranda 4894* (MEXU); Cuichapa, *Rosas 910* (XAL); Municipio de Dos Ríos, *Ventura 930* (MO); vicinity Fortín, *Croat 39414* (MO); Fortuno, Coatzacoalcos River, *Williams 8940* (MICH, US); Hidalgotitlán, *Dorantes 2862, 3099* (XAL); *Valdivia 23, 138, 614, 689, 799, 870, 1038, 1045, 1115, 1315, 1343, 1622* (XAL); *171, 236* (XAL, MO); *191, 309, 476, 533* (MEXU); *222, 291, 421, 731, 1165, 1285, 1674* (MO); *275, 667, 907, 931, 1196* (XAL, MEXU, MO); *458, 1094* (XAL, MEXU); *Vazquez 582* (BM, MO, XAL); vicinity Huatusco, *Croat 44000* (MO); *Ghiesbreght 70* (P); *Moore & Bunting 8867, 8868* (CU); vicinity Ixhuatlán, *Lot 869* (CAS, MEXU); SE of Jalapa, *Barkley et al. 2596* (MEXU, TEX); Lake Catemaco, *Boege 1257* (MEXU); Minatitlán, *Gilly & Hernandez 253* (MICH); Naolinco, *Ortega 556* (MO); Nautla, *Fay & Calzada 925* (XAL); Orizaba, *Botteri & Lumichrast 1602* (P); *Croat 39548* (MO); *Muller 1314, 1335* (NY); Palmasola, *Nevling & Gomez-Pompa 1274* (MO, XAL); Rancho Viejo, *Purpus 15711* (UC); San Andrés Tuxtla, *Calzada 455* (MEXU); *Dressler & Jones 8* (MICH, NY, UC); *Hernandez & Vazquez 552* (MEXU); *Moore & Cetto 6232* (BH, MEXU); *Soto et al. 16* (F, MO, XAL); above San José de Gracia, *Croat 39611* (MO); Santiago Tuxtla, *Sousa 2158, 2373* (MEXU); E slopes of Sierra de Los Tuxtla, *Cochrane & Cochrane 8625* (MO); Barra de Sontecomapan, *Hernandez 608* (MEXU); Tapalapa, *Gomez-Pompa 5105* (MO); Zacualpán, *Purpus 11130* (MY, UC). YUCATÁN: Chichén Itzá, *Steere 1124* (MICH); *Thompson 437, 438* (MO); S of Mérida, *Gaumer 741* (F, MO); *Schott 638* (F); N of Muna, *Luteyn 2528* (DUKE); Córdoba, *Bourgeau 1787* (MEXU, P).

NICARAGUA. CHONTALES: N of Cuapa, *Atwood & Neill AN35* (MO); road from Juigalpa to La Libertad, *Stevens 4030* (MO). ESTELÍ: N of entrance to Estelí, *Stevens 5786, 9095* (MO). ZELAYA: near El Recreo, *Atwood & Neill AN233* (MO); S of Siuna, *Neill 4226, 4289, 4521* (MO); *Stevens 7377, 7383, 7386, 8736, 8753, 8755* (MO).

b. Anthurium schlechtendalii ssp. **jimenezii** (Matuda) Croat, comb. nov. *Anthurium jimenezii* Matuda, Anales Inst. Biol. Univ. Nac. México 32: 147. 1961. TYPE: Mexico. México: Barranca de Zacualpan on volcanic rocks, 1,300 m elev., *Matuda 37245* (MEXU, holotype).

Usually terrestrial or on rocks, usually 0.5–1 m tall; stems less than 30 cm long, ca. 3–4 cm diam.; roots moderately thick, directed downward, sometimes curved upward; cataphylls coriaceous, 6–7 cm long, acute at apex with minute subapical apiculum, drying reddish-brown, remaining ± intact in upper nodes, ultimately deciduous. LEAVES erect-spreading; petioles 2–15 cm long, 8–9 mm diam., subquadrangular, broadly and sharply sulcate; geniculum 1–1.5 cm long; blades oblanceolate to lanceolate, gradually acuminate at apex (the acumen apiculate), obtuse to narrowly rounded at base, broadest at middle, 36–104 cm long, 6–32 cm wide; both surfaces semiglossy, lower surface sometimes having a bluish-green color; midrib slightly raised at base, more acutely raised midway and sunken at apex above, quadrangular and prominently raised below, becoming convex at apex; primary lateral veins 9–14 per side, departing midrib at 50° angle, raised above, usually raised below, arcuate-ascending; interprimary veins weakly sunken above, prominulous below; lesser veins obscure above, visible below; collective vein arising from one of the primary lateral veins in the lower half of blade, 2–4 mm from margin, flat above, prominulous below. INFLORESCENCE erect, shorter than leaves; peduncle 10–54 cm long, 3–5 mm diam., terete, longer than petioles; spathe subcoriaceous, green weakly tinged with purple (B & K Yellow-green 6/5), 4–8.5 cm long, 1–2.5 cm wide, lanceolate, oblique and narrowly acuminate at apex, subcordate at base, broadest just above base, inserted at 30° angle on peduncle;

spadix usually sessile, greenish tinged with purple (B & K Yellow-green 6/5), 3.5–14 cm long, 5–10 mm diam. at base, 2–5 mm diam. at apex; the flowers rhombic to sub-4-lobed, 2.7–2.8 mm long, 2.3–2.5 mm wide, the sides straight to jaggedly sigmoid; 11–12 flowers visible in the principal spiral, 7–8 flowers visible in the alternate spiral; the tepals matte, obscurely and sparsely punctate with numerous, irregular droplets at anthesis, lateral tepals 1.5 mm wide, the inner margin broadly rounded, the outer margin 3–4 sided; pistils weakly emergent, medium green; the stigma 0.5 mm long, oblong-elliptic; stamens emerging in a prompt complete sequence from the base; the anthers creamy white, leaning over edge of pistol, 0.8 mm long, 1 mm wide; thecae oblong-elliptic, slightly divaricate; pollen white. INFRUCTESCENCE pendent; berries red, oblong-ellipsoid, rounded at apex, 11 mm long, 9 mm wide; mesocarp with raphide cells dense and numerous throughout; seeds 2, oblong-ellipsoid, tan, flattened, 6 mm long, 4 mm wide, 2 mm thick with pale, punctiform raphide cells, encased in a slender, sticky, gelatinous, apically elongated envelope. Fig. 180.

Anthurium schlechtendalii ssp. *jimenezii* is endemic to Mexico and is restricted to Guerrero and southern Oaxaca in seasonally very dry forests at 250 to 1,350 m elevation.

Subspecies *jimenezii* is recognized by its exclusively terrestrial or rupicolous habit, its thick, oblanceolate leaf blades with usually free-ending primary lateral veins, its purplish spadix, green, lanceolate spathe, and red berries.

This subspecies is geographically isolated from the typical subspecies of *A. schlechtendalii,* which is found in northern Oaxaca and also on the eastern side of the Isthmus of Tehuantepec but not in eastern Oaxaca. Subspecies *jimenezii* differs from the typical subspecies in being generally smaller, by occurring exclusively on rocks and in seasonally much drier habitats, and by having usually thicker leaf blades. Matuda (1961) stressed that the taxon has peduncles relatively much longer than typical in *A. schlechtendalii.* While it is generally true that the inflorescences of ssp. *jimenezii* are commonly as long as or longer than the leaves they may also be much shorter than the leaves.

Subspecies *jimenezii* is also similar to *A. halmoorei,* which differs in having an ovate to ovate-elliptic spathe and mature berries that are pale greenish-yellow. Also similar is *A. nizandense,* which is endemic to southern Guerrero and southern Oaxaca. *Anthurium nizandense* differs in having proportionately much longer petioles and elliptic to oblong-elliptic blades that are matte on the lower surface. In *A. nizandense* the blades are 1.3–2.5 times longer than the petioles whereas in *A. schlechtendalii* ssp. *jimenezii* the leaf blades are usually 6 to 10 times longer (rarely only as little as 3 times longer).

MEXICO. GUERRERO: El Ocotito, between Tierra Colorada and Agua de Obispo, *Crisman & Willis 199* (MICH); Carreceras, *Hinton et al. 10098* (US); Trincheras, *Hinton et al. 10125* (K, US); Malinaltenango, S of Zacualpan, *Matuda 37245* (MEXU); beyond Acapulco to Chilpancingo, *Moore 5099* (BH); between Acahuizotla and Agua de Obispo, *Moore 5120* (BH, UC); highway above Acahuizotla, *Moore 6957* (BH); Tierra Colorada, *Rodriguez 51* (US); *Rzedowski 22809* (MICH, US). OAXACA: N of Putla de Guerrero, *Croat 45926* (MO); between Oaxaca and Pochutla, S of Miahuatlán, *Croat 46093* (MO); N of Pluma Hidalgo, *Croat 46142* (MO); vicinity Santa Rosa, Km 195 on road to Oaxaca-Puerto Escondido, *Rzedowski 19592* (MEXU).

Anthurium schottianum Croat & Baker, Brenesia 16 (Supl. 1): 83. 1979. TYPE: Costa Rica. Limón: ca. 1 mile N of Bribrí, ca. 40 miles SW of Limón; steep ravine above Río Catarata, 50–100 m elev., *Croat 43247* (MO-2584489, holotype; CR, F, K, SEL, US, isotypes; Live at MO).

Large terrestrial; stems usually less than 50 cm long, 3–5 cm diam.; leaf scars conspicuous, 2–4 cm wide; roots few, green, ca. 5 mm diam. descending, often short and blunt; cataphylls coriaceous, dark purple, 9–12 cm long, apiculate at apex, drying brown with tinges of reddish-purple, subpersistent. LEAVES with petioles erect to spreading, 40–150 cm long, 5–8 mm diam., shallowly sulcate to flat adaxially, rounded with a few faint ridges abaxially, tinged dark purple from the base; geniculum 2–3 cm long; blades ovate, gradually acuminate at apex (the acumen long apiculate, turned down), lobed at base, 44–100 cm long, 33–50 cm wide, broadest near point of petiole attachment, the margin shallowly undulate; the anterior lobe 32–80 cm long with margins convex; posterior lobes 12–19 cm long; the sinus usually narrowly triangular, sometimes closed, acute at apex; the upper surface matte to semiglossy, lower surface semiglossy; the midrib acutely raised above, diminishing toward apex and sunken, prominently raised below; basal

FIGURES 176–179. 176. *Anthurium seibertii* Croat & Baker, *Croat 26976* (Type).—177–178. *Anthurium seibertii* Croat & Baker, *Croat 48568*.—179. *Anthurium seleri* Engl., *Croat 46505*.

FIGURES 180–183. 180. *Anthurium schlechtendalii* ssp. *jimenezii* (Matuda) Croat, *Croat 45926*.—181. *Anthurium seleri* Engl. (Cultivated at MEXU).—182–183. *Anthurium silvigaudens* Standl. & Steyerm., *Croat 41173*.

veins 5–8 pairs, not coalesced, raised above and below; primary lateral veins 9–20 per side, departing midrib at 35°–50° angle, slightly arcuate-ascending, faintly loop-connecting, sharply raised above and below; interprimary veins very few, slightly raised near apex of leaf above, raised below; secondary veins mostly flat above, in part raised, especially in posterior lobes, somewhat raised below; tertiary veins scarcely visible above, scarcely raised below; collective vein usually arising from the second basal vein, inconspicuous, slightly sunken above, slightly raised below, 2–6 mm from the margin. INFLORESCENCE erect, much shorter than the leaves; peduncle sometimes absent or to 20 cm long, 4–5 mm diam., dark purple, terete; spathe coriaceous, dark purple with green splotches (B & K Red-purple 2/7.5), ovate-lanceolate, 6.5–15 cm long, 1.6–3.5 cm wide, broadest at base, abruptly acuminate at apex, rounded to subcordate at base, stiffly curled back lengthwise, frequently twisted at anthesis, inserted at ca. 45° angle on peduncle; spadix purple (B & K Purple 2/7.5), 4–14 cm long, 7–9 mm diam. at base, 4–5 mm diam. at apex; flowers square, 2.6–3 mm long, 1.5–3.5 mm wide, the sides nearly straight; 4–6 flowers visible in the principal spiral, 5–8 flowers visible in the alternate spiral; tepals matte, densely punctate, minutely papillate, the lateral tepals to 1.9 mm wide, the inner margin straight to convex, held flat against pistil; pistil violet-purple, minute and barely exposed 1 or 2 spirals ahead of emerging stamens, gradually larger as stamens emerge; stigma a dry, linear slit when stamens are emerging; stamens emerging slowly from the base, exserted on short filaments which retract to hold anthers in a tight cluster around the pistil; filaments flattened, milky, the exposed part ca. 0.3 mm long. 0.6–0.7 mm wide; anthers yellow, held above pistil, 0.5–0.6 mm long, 0.7–0.9 mm wide; thecae ellipsoid, scarcely divaricate; pollen yellow (B & K Yellow 9/5), drying pale yellow. INFRUCTESCENCE pendent; spathe usually persisting; spadix to 35 cm long, to 2.5 cm wide, the apical one half to one third often not developing berries; berries obovoid, acute to rounded at apex, pinkish with a metallic sheen, darker in the apical third, 9–10 mm long; seeds 2, tan, to 6 mm long, 5 mm wide, flattened, ca. 2 mm thick. Figs. 174 and 175.

The species is known only from the region of premontane wet forest-basal belt transition in extreme southwestern Costa Rica at elevations of less than 100 m. It will no doubt be found elsewhere in Costa Rica and Panama on the Atlantic Slope.

Anthurium schottianum is a member of section *Pachyneurium* and is distinguished by its large, thin, ovate leaf blades with scarcely any posterior rib (i.e., all basal veins are free to the petiole) and by its short peduncle, its purple spadix and its ovate-lanceolate, often purplish, frequently twisted spathe.

COSTA RICA. LIMÓN: near the Río Catarata between Bribrí on the Río Sixaola and the Caribbean costal plain, *Baker & Burger 69* (MO); *Burger et al. 10391* (F, MO); NE of Bribrí, ca. 40 mi SW of Limón, *Croat 43247* (CR, F, K, MO, SEL, US); N of Bribrí on banks of Río Catarata, *Utley 5500* (DUKE).

Anthurium seibertii Croat & Baker, Brenesia 16 (Supl. 1): 85. 1979. TYPE: Panama. Chiriquí: wooded slopes on Cerro Horqueta, 1,650 m, *Croat 26976* (MO-2251853, holotype; CR, F, NY, PMA, US, isotypes; Live at MO).

Epiphyte; stems thick, short, 3–6 cm diam.; leaf scars mostly hidden, ca. 2 cm wide; roots numerous, descending, ca. 6 mm diam., green with crusty tan epidermis; cataphylls coriaceous, 12–21 cm long, caudate-acuminate at apex, the apiculum ca. 5 mm long, drying tan (B & K Yellow-red 8/5), splitting at base, the apex remaining ± intact. LEAVES held stiffly erect-spreading; petioles 10–55 cm long, 6–10 mm wide, ± quadrangular, 5-ribbed with 3 ribs on the abaxial side, sometimes with 2 additional ribs on the lower corners; geniculum 1.5–3 cm long, ribbed as the petiole; blades strap-shaped, gradually acuminate at apex, obtuse to slightly rounded at base, 45–85 cm long, 4–16 cm wide, broadest at middle, the margin flat to slightly undulate; upper surface semiglossy, lower surface matte to semiglossy; midrib convexly raised above, diminished at apex, sharply and obtusely raised below; primary lateral veins numerous on each side, departing midrib at 50°–60° angle, sunken above, sharply raised below, arcuate-ascending, prominently loop-connecting; interprimary veins numerous, slightly sunken above, prominulous below; secondary veins flat above, flat or slightly raised and darker below; collective vein arising from near base, about as prominent as the primary lateral veins, sunken above, prominently raised below, 2–7 mm from margin. INFLORESCENCE erect or spreading at anthesis, ca. two thirds as long as leaves; peduncle 30–60 cm

long, 6–10 mm diam., terete with a single dorsal rib, sometimes tinged purplish; spathe medium thick, green or green tinged with purple (B & K Yellow-green 7/10), oblong-lanceolate, 10–17 cm long, 2.5–4.3 cm wide, broadest at point of attachment, gradually and narrowly long-acuminate at apex, rarely short-acuminate, rounded at base, inserted at 50° angle on peduncle, often becoming coiled; stipe ca. 13 mm long in front, 1 mm long in back, 8 mm wide, tinged purple; spadix violet-purple (B & K Blue-purple 2/10), 10–20 cm long, 7–13 mm diam. at base, 5–6 mm diam. at apex; flowers 4-lobed, 2–2.5 mm in both directions, the sides jaggedly sigmoid, 7–9 flowers visible in principal spiral, 7–10 flowers visible in alternate spiral; tepals matte, the lateral tepals ca. 1.5 mm wide, the inner margin straight; the pistil emergent, orange-yellow; the stigma ca. 0.7 mm long, 0.2–0.3 mm wide, with conspicuous stigma droplets for several days before stamens emerge; stamens emerging ± rapidly from the base, the lower fourth with stamens emergent while apical flowers still are producing droplets on the stigmas; anthers pale orange, held just above tepals in a tight cluster, ca. 0.5 mm long, 1 mm wide; the thecae ellipsoid, scarcely divaricate; pollen white. INFRUCTESCENCE pendent; spathe often missing; spadix usually 22–30 cm long, ca. 2 cm wide; berries orange, obovoid, flat to rounded at apex, 10–12 mm long; mesocarp orange, mealy, sweet tasting but pungent; seeds 2, ± oblong with rounded corners, ca. 5 mm long, 4 mm wide, 2 mm thick. Figs. 176, 177, and 178.

Anthurium seibertii is known from higher altitudes in Chiriquí Province (1,300–2,000 m) and from one collection at 1,040 m in San José Province of Costa Rica (*Skutch 2626*, MO, US).

The species is a member of the section *Pachyneurium* and is very similar to *A. protensum*. They share similar strap-shaped leaves, pale violet-purple spadices and orange berries. *Anthurium protensum* differs in having a nearly terete petiole while *A. seibertii* has petioles that are prominently ribbed abaxially and rectangular. *Anthurium protensum* also has leaves that are usually pendent and are generally smaller than those of *A. seibertii*.

COSTA RICA. SAN JOSÉ: El General, 1,040 m, *Skutch 2626* (F, MO).

Anthurium seleri Engl., Bot. Jahrb. Syst. 25: 459. 1898. TYPE: Guatemala. Huehuetenango: near Chaculá, *Seler 2643* (B, holotype).

Anthurium andresloviense Matuda, Anales Inst. Biol. Univ. Nac. México 36: 108. 1966. TYPE: Mexico. Oaxaca: San Andrés Lovene, Munic. Miahuatlán (N of Pluma Hidalgo), 1,200 m elev., *MacDougall 384* (MEXU, holotype; F, isotype).

Terrestrial; internodes and leaf scars obscured by cataphylls and roots; roots numerous, medium thick, descending; cataphylls subcoriaceous, 6–11 cm long, sometimes faintly tinged reddish at apex, sometimes with long hair-like subapical apiculum, drying reddish brown, splitting at base, remaining intact at apex and persisting. LEAVES with petioles erect to spreading, (7)14–48 cm long, 4–6 mm diam., sharply and shallowly sulcate; geniculum 1.4–1.6 cm long; blade moderately thick, narrowly triangular to oblong-lanceolate or oblong-lanceolate with hastate posterior lobes, gradually acuminate at apex, usually broadly lobed, sometimes deeply lobed or ± rounded to truncate at base, (9)24–50 cm long, (5)10–50 cm wide, broadest at base; anterior lobe (8.5)25–41 cm long, margins convex to straight; posterior lobes 6–18 cm long, from sinus to outermost point; the sinus usually parabolic, sometimes arcuate with petiole decurrent, broader than deep, rounded at apex; the upper surface matte to semiglossy, the lower surface matte; midrib bluntly and weakly raised above, convexly raised below; basal veins 2–5 pairs, the second to fifth coalesced to 8 cm; posterior rib straight, naked, turned up on outer margin; primary lateral veins 9–11 per side, departing midrib at 45°–50° angle, usually straight, loop-connecting to collective vein, sunken and nearly obscure above, flat below; collective vein arising from one of the lowermost basal veins, sunken above, flat below, 2–6 mm from margin. INFLORESCENCE erect-spreading, longer than leaves; peduncle 25–50(86) cm long, terete, sometimes faintly tinged with purple; spathe moderately thin, lanceolate, pale green, tinged reddish at base, 5–9 cm long, 0.9–1.5 cm wide, long-acuminate at apex, acute to rounded at base, inserted on peduncle at 50°–70° angle; stipe 4–20 mm long in front, 1–15 mm long in back; spadix green, tinged red-violet along inner margins of tepals, 6–13 cm long, 6–8 mm diam. at base, 2–4 mm diam. at apex; flowers rhombic to sub-4-lobed, 3.5–3.7 mm long, 3–3.5 mm wide, the sides ± straight to gradually sigmoid; 4–5 flowers visible in the principal spiral, 4–10 flowers visible in the alternate spiral; tepals matte, minutely punctate, abundant droplets when stamens begin to emerge, lateral tepals 1.4–1.6 mm wide, the inner margin straight to convex, ± transparent; pistils emergent to 4 mm,

white to pale green with minute purple punctations; stigma linear, ca. 0.5 mm long; stamens emerging slowly from the base in a ± complete sequence, lateral stamens first followed by alternates, the basal spirals complete as lateral stamens emerge above middle, exserted on short filaments, ca. 0.2 mm long, soon retracting and held in a circle at edge of pistil; anthers tan, 0.5–1 mm long, 0.7–1.2 mm wide, inclined over pistil; thecae ellipsoid, slightly divaricate; pollen white to pale yellow. INFRUCTESCENCE pendent; berries red, obovoid, 6–7 mm long, 4 mm wide. Figs. 179, 181, and 184.

Anthurium seleri is known primarily from a relatively small geographic area ranging from eastern Mexico (central Chiapas) to adjacent areas of west central Guatemala in the Department of Huehuetenango at elevations from 700 to 1,900 m. The species has also rarely been collected in southern Oaxaca in the Sierra Madre del Sur, and while these appear to be outlying populations, both regions probably consist of vegetation that is "bosque pino-encino" on the Mexican vegetation maps, which are generally quite arid. Plants are usually found growing on rocks or on steep cliffs in shaded canyons but have also been found in open almost deforested areas.

The species is a member of section *Belolonchium* and is recognized by its coriaceous blades, which are either oblong or narrowly triangular with usually little or no development of posterior lobes or with the posterior lobes directed outward almost at a 90° angle from the midrib. An extreme development of the posterior lobes is found in some collections from the northern and western part of the range of the species and a few collections such as *Carlson 1523, Reko 6203,* and *MacDougall 686* have posterior lobes of the blade almost as long as the anterior lobe.

An interesting feature exhibited by *A. seleri* is that while most collections dry matte and greenish, some collections, such as *Croat 46505,* dried brown with the surfaces glossy. Since no other differences were apparent it is assumed that these differences were a matter of differences in drying.

Anthurium seleri collections with well developed posterior lobes can be confused with collections of *A. berriozabalense.* See the discussion following that species for ways of distinguishing the two species.

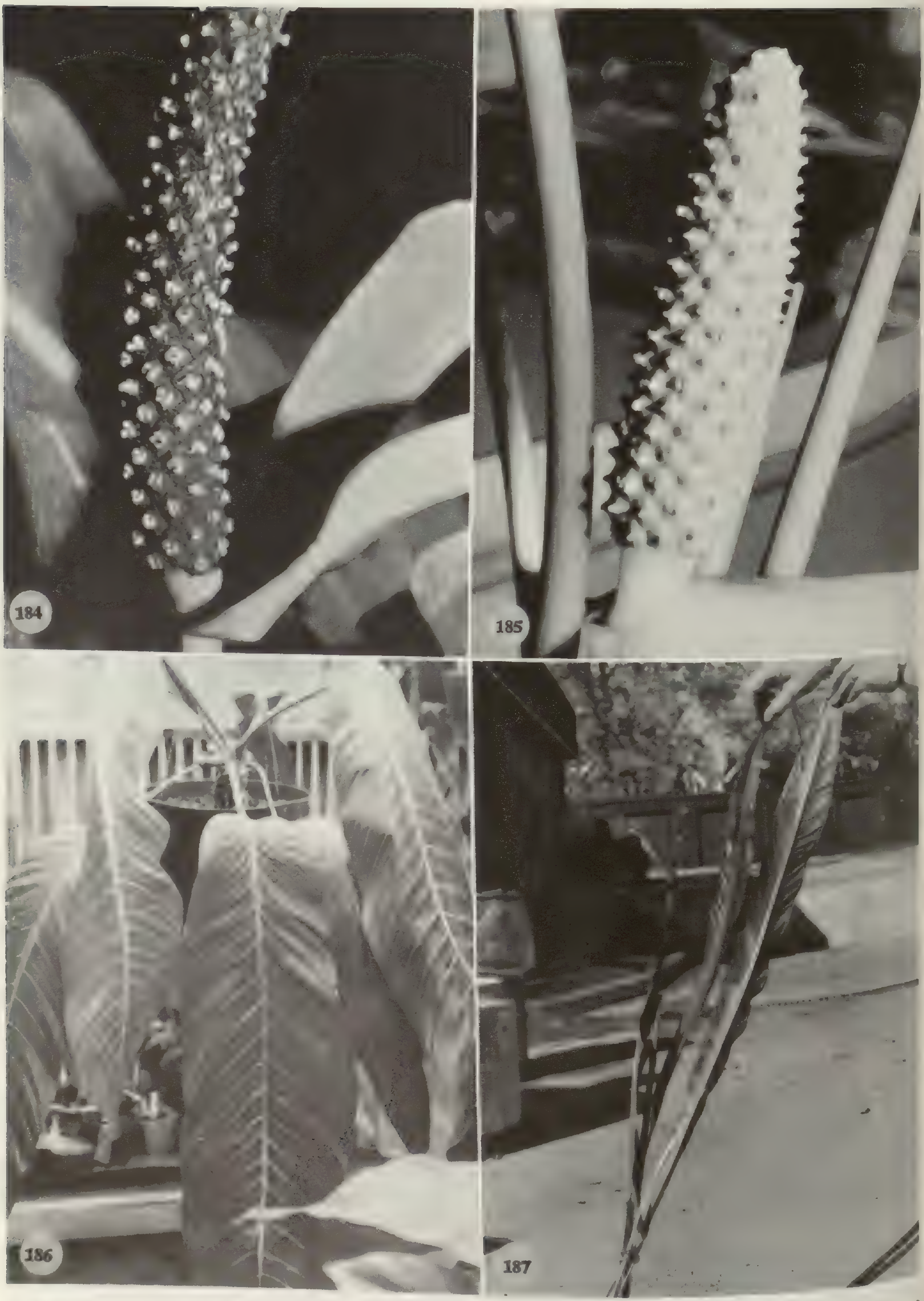
The designated type of *A. andresloviense* (*MacDougall 384*) represents a mixed collection. Specimens from MEXU, numbers *59608* and *59838* correspond to the type description and to the photograph, respectively, presented by Matuda. Another MacDougall collection of *384* has been assigned the number *384A*. It is actually *A. ovandense.*

As mentioned in the introductory paragraph, MacDougall had often recollected what he believed to be the same plants again; when he did, he had the unusual practice of assigning them the same number as he did the first time he collected the plant. In this case the plants he recollected were in fact of some other species, even though they both have similar leaves and were both collected at San Andrés Lovene.

MEXICO. Cultivated Miami, Florida, origin Mexico, *Croat 44760* (MO). CHIAPAS: Aguatenango, *Breedlove 6612* (DS, MICH); Arriaga, *Breedlove & Thorne 30579* (DS); between Bochil and Sayulo, *MacDougall 686* (MEXU); Cintalapa, SE of Cerro Baúl, *Breedlove 24716* (DS); Cintalapa, *MacDougall 703* (NY); vicinity Comitán, *Webster et al. 12897* (DAV, MO, US); La Independencia, *Breedlove 33460* (DS); Las Margaritas, *Breedlove 34732* (CAS, DS), Ocozocoautla de Espinosa, *Breedlove 28997* (DS); *Breedlove 29187, 32876* (CAS, DS); *Carlson 1523* (DS, UC); *Croat 40541* (MO); *MacDougall H260* (NY); Pueblo Nuevo Solistahuacán, *Thorne & Lathrop s.n.* (LL); *40392* (DS, RSA); vicinity Teopisca, *Croat 46505* (MO); *Breedlove 26201* (CAS, DS, DUKE, LL, MICH, MO); Venustiano Carranza, *Laughlin 1947* (CAS, DS); *Breedlove 10564* (CAS, DS, LL, MICH); *Breedlove 11187* (CAS, DS, LL); *Raven & Breedlove 20104* (CAS, DS, LL). OAXACA: Pochutla, *Reko 6204* (GH); San Andrés Lovene, *MacDougall 384* (MEXU).

Anthurium silvigaudens Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 69. 1940. TYPE: Guatemala. Alta Verapaz: near Tactic, elev. ca. 1,500 m, *Standley 70505* (F, holotype).

Epiphytic or usually terrestrial to 120 cm tall; stems green, 2 cm diam.; internodes 1–2 cm long; leaf scars 1.4 cm wide; roots medium thick, pale green, directed downward; cataphylls subcoriaceous, 6–13 cm long, the apex round with a minute apiculum, drying tan (B & K Yellow-red 9/10), weathering to linear fibers and persisting. LEAVES usually erect; petioles 23–54 cm long, 5–6 mm diam., terete; geniculum 1.5–2 cm long; blades ovate, moderately thin, gradually acuminate at apex, lobed at base, 22–48 cm long, 13–31 cm wide, broadest just below middle; anterior lobe 17–33 cm long, the margins convex; posterior lobes 8.2–15 cm long, directed upward; the sinus hippocrepiform to spathulate, round to acute at apex; both surfaces matte (cells on lower surface glistening and weakly papillate); the midrib sharply raised above, diminishing at center,



FIGURES 184–187. 184. *Anthurium seleri* Engl., *Croat 44760*.—185. *Anthurium silvigaudens* Standl. & Steyerm., *Croat 41475*.—186. *Anthurium spectabile* Schott, *Croat 1-26-78N*.—187. *Anthurium spathiphyllum* N. E. Brown, *Croat 44309*.

sunken at apex, bluntly raised below; basal veins 4–7 pairs, the first and second (sometimes third) free to base, the third to seventh coalesced 1–3.5 cm; posterior ribs naked, upturned; primary lateral veins 4–6 per side, departing midrib at 45°–55° angle, sunken in valleys above, raised below, straight or arching to collective vein; lesser veins prominulous above and below; collective vein arising from first or second basal vein, 4–10 mm from margin. INFLORESCENCE erect, much shorter than leaves; peduncle 3.5–10 cm long, 6–7 mm diam., terete, shorter than petioles; spathe subcoriaceous, medium green (B & K Yellow-green 7/10), ovate, 5.5–8.5 cm long, 4.3–6 cm wide, broadest just above point of attachment, abruptly acuminate at apex, cordate at base, inserted at 40° angle on peduncle; the stipe 7–15 mm long in front, 4 mm long in back, tapered at base of spadix, medium green; spadix medium green (B & K Yellow-green 7/2.5), 2.5–5.2 cm long, 1.4–2 cm diam. at base, 5–8 mm diam. at apex; flowers rhombic to sub-4-lobed, 3.5–4 mm long, 3.6–4 mm wide, the sides sigmoid to jaggedly sigmoid, sometimes broadly rounded parallel to the spirals; 5 flowers visible in the principal spiral, 7 flowers visible in the alternate spiral; tepals matte to semiglossy, lateral tepals 2.2–2.5 mm wide, the inner margin broadly rounded and turned up against the pistil; the pistil emergent to ca. 0.7 mm, darker green than tepals; stigma 0.3 mm long, round, brushlike, glistening; stamens emerging promptly throughout the spadix (sometimes beginning at apex), the lateral stamens emerging throughout before the alternates emerge, the third and fourth stamens following in rapid sequence after 1 or 2 days; filaments exserted, 0.5 mm long, translucent; anthers pale yellow, retracted to upper edge of tepals, 0.7–0.8 mm long, 1 mm wide; thecae oblong-ellipsoid, slightly divaricate; pollen creamy white. INFRUCTESCENCE erect; spathe persistent; spadix 4–6 cm long, 2.5–4 cm diam.; berries obovoid, vermillion-coral (see *Steyermark 51703*), rounded at apex, 11–13 mm long, 6–8 mm diam.; seeds 2, oblong-obovoid, weakly flattened, 5.5–7.5 mm long, 3.5–4 mm wide, 2–2.5 mm thick. Figs. 182, 183, and 185.

Anthurium silvigaudens is found in Guatemala and Honduras at 1,500 to 2,000 m elevation in tropical wet forest. In Guatemala it has been collected in the Department of Alta Verapaz in the vicinity of Purulhá and Tactic as well as in the Department of Huehuetenango in the Sierra de los Cuchumantes. It is certainly expected to be found in the Department of Quiché as well. In Honduras it was collected near Lepaera.

The species is characterized by its moderately thin, ovate, prominently lobed leaf blades with weakly impressed secondary and tertiary veins, by its short peduncle, its ovate, cordate, green spathe, stubby greenish spadix, and orange-red berries. Its sectional placement is uncertain but may best be placed in section *Belolonchium*.

Although Standley and Steyermark in the type description compare the species with *A. fraternum* Schott it bears little resemblance or relationship with that species except for having a blade of similar shape. It is unlikely that the species is even in section *Calomystrium*. It is apparently not closely related to any other species in Central America.

GUATEMALA. ALTA VERAPAZ: road to El Estor, E of Highway 14 to Cobán, *Croat 41440, 41475* (MO); vicinity Tactic, *Standley 70505* (F). BAJA VERAPAZ: No other location, *Molina & Molina 27728* (F); *Tuerckheim 1825* (US); NE of Purulhá, *Croat 41306* (MO); S of Purulhá, *Croat 41173, 41753* (MO). HUEHUETENANGO: E of Las Palmas, Sierra de los Cuchumantes, *Steyermark 51703* (F).

HONDURAS. LEMPIRA: vicinity Lepaera, *Molina 24135* (F).

Anthurium spathiphyllum N. E. Brown, Gard. Chron. 652. 1877. TYPE: Origin unknown: Hort. Kew, Nov. 8, 1876, *N. E. Brown s.n.* (K).

Epiphyte; stems ca. 10 cm long, ca. 2 cm diam.; covered by numerous, moderately thick, fuzzy roots; cataphylls chartaceous, 7–8 cm long, cuspidate at apex with long, subapical apiculum ca. 1.5 cm long, pale tan (B & K Yellow 9/7.5), weathering into coarse, longitudinal fibers and persisting. LEAVES spreading; petioles usually triangular or sharply 3–5 ribbed; geniculum 7–10 cm long, conspicuously bulging adaxially; blades linear to linear-lanceolate, subcoriaceous, 46–80 cm long, 5.5–12.5 cm wide, broadest at middle, the margins broadly undulate; both surfaces semiglossy; the midrib scarcely raised and broad at base, narrowing and convexly raised at middle, acute nearly to apex, sunken at apex above, sharply raised below; primary lateral veins 20–30 per side, departing midrib at 40°–45° angle, straight to collective vein, sunken above, raised below; interprimary veins flat to scarcely sunken above, prominulous below; collective vein

arising from near the base, 3–6 mm from the margin, sunken above, raised below. INFLORESCENCE spreading, shorter than leaves; peduncle flattened, 2–4 ribbed, 33–48 cm long, 1–1.5 cm wide, 2 times longer than petioles; spathe coriaceous, green, lanceolate to broadly lanceolate 6.5–8 cm long, 1.7–3 cm wide, broadest below middle, short acuminate at apex, rounded at base, inserted at 50° angle on peduncle; spadix pale yellow to creamy white, (1.7)3–4 cm long, 0.9–1.1 cm diam. midway; flowers 4-lobed, ca. 1.4 mm long, 2.2 mm wide, the sides sigmoid; ca. 12 flowers visible in principal spiral, 15 flowers visible in the alternate spiral; tepals matte, the lateral tepals 0.7 mm wide, the inner margins straight; pistils emergent, pale yellow; stigma minute, drying before stamens emerge; lateral stamens scattered throughout before alternates appear, exserted on fleshy filaments, held over and obscuring pistil; thecae oblong, not divaricate; pollen pale yellow fading to cream. INFRUCTESCENCE unknown. Fig. 187.

Anthurium spathiphyllum is known from Costa Rica to Panama from sea level to 380 m (with the exception of *Croat 35571,* which was collected at 1,350 m elevation) on the Atlantic slope in wetter parts of tropical moist forest and in premontane wet and tropical wet forest life zones.

The species can be recognized by its epiphytic habit, chartaceous leaves, usually triangular, sometimes 3–5 ribbed petiole, lanceolate to broadly lanceolate cucullate spathe, and short, scarcely tapered, pale yellow spadix.

Anthurium spathiphyllum is in section *Pachyneurium* and is most closely related to *A. cuneatissimum.* The latter species differs in having fewer, less sunken primary lateral veins (commonly 10–15 versus 20–30 for *A. spathiphyllum*) and in having a spathe that is ovate and about as long as the spadix (versus lanceolate to broadly lanceolate and about two times longer than the spadix in *A. spathiphyllum*).

COSTA RICA. ALAJUELA: N of San Miguel, *Croat 35651* (MO). HEREDIA: upstream on Rio Puerto Viejo, *Burger & Matta 4258* (F); N of Vara Blanca, *Croat 35571* (MO). LIMÓN: Hacienda Tapezco-Hda. La Suerte, W of Tortuguero, *Davidson & Donahue 8954* (MO); Pandora, *Ocampo 1987* (MO); W of Dos Bocas, beside Río Parismina, *Lent 2444* (F).

NICARAGUA. ZELAYA: N of Limbaika, *Stevens 8255* (MO); between Rosita and Puerto Cabezas, SW of Río Kukalaya, *Stevens 8504* (MO).

Anthurium spectabile Schott, Oesterr. Bot. Z. 8: 181. 1858. TYPE: Costa Rica. Cartago: Volcán Turrialba, *Wendland 506* (GOET, 2 sheets).

Anthurium longispathum Schott, Prod. Aroid. 520. 1860. TYPE: Costa Rica. Turrialba, *Oersted* (Photo of Schott Aroid Drawing #707, NYBG Neg. #N.S. 3952).

Epiphyte; cataphylls subcoriaceous, 17–38 cm long, obtuse at apex with subapical apiculum ca. 2 mm long, drying light tan (B & K Yellow-red 9/10), splitting at base, the apex remaining intact, persisting. LEAVES spreading; petioles quadrangular, 14–53 cm long, 7–10 mm wide, broadly sulcate adaxially, with a faint convex rib abaxially; geniculum 1.3–1.9 cm long; blades oblong-lanceolate to oblong or oblong-triangular, moderately thick, long-acuminate at apex, rounded to truncate at base, 37–135(160) cm long, 8–35(45) cm wide; the upper surface semiglossy to glossy, the lower surface glossy; the midrib acutely raised above, broad at base, narrow and sunken at apex, convexly raised below becoming more acute at apex; primary lateral veins numerous, departing midrib at 45° angle, raised above and below; lesser veins conspicuous but not raised above and below; collective vein arising from one of the primary lateral veins in the basal one half of the blade, sunken above, raised below, 2–3 mm from margin. INFLORESCENCE spreading, shorter than leaves; the peduncle 13–25 cm long, terete; spathe subcoriaceous, narrowly ovate to oblong-lanceolate, green or violet-purple inside, green outside, 10.5–32 cm long, 3–7 cm wide, acuminate at apex, rounded to subcordate at base, inserted at 45° on peduncle, usually twisted or coiled and strongly reflexed; spadix yellow-green, 16–38 cm long, ca. 9 mm diam. at base, 7 mm diam. at apex; the flowers rhombic to 4-lobed, 2.5–4 mm in both directions, the sides sigmoid; 7–11 flowers visible in principal spiral, ca. 9 flowers visible in the alternate spiral; tepals matte to semiglossy, 2–2.5 mm long, ca. 2.7 mm wide, the inner margins convex; pistils emergent, green, violet-purple at apex; stigma ca. 1 mm long, elliptic; stamens emerging promptly throughout length of spadix in a complete sequence; anthers held around exserted pistil; thecae narrowly ovoid, slightly divaricate; pollen cream-colored. INFRUCTESCENCE with spadix to 50 cm long; berries oblong-linear, probably orange at maturity, 10–14 mm long, ca. 3.5 mm diam., tapered to a blunt apex; seeds 2, 3.4–

FIGURES 188–191. 188. *Anthurium standleyi* Croat & Baker (Cultivated at KEW).—189. *Anthurium standleyi* Croat & Baker, *Croat 43431*.—190. *Anthurium subcordatum* ssp. *chlorocardium* (Standl. & L. O. Wms.) Croat, *Allen et al. 6075* (Type).—191. *Anthurium subcordatum* Schott, *Croat 42500*.

FIGURES 192–195. 192. *Anthurium subovatum* Matuda, *Croat 39815*. — 193. *Anthurium subsignatum* Schott, *Croat 36455*. — 194. *Anthurium subsignatum* Schott (Cultivated at KEW). — 195. *Anthurium tenerum* Engl., *Croat 47089*.

FIGURES 196–199. 196. *Anthurium subcordatum* Schott, *Croat 42500.*—197. *Anthurium spectabile* Schott, *Croat 46968.*—198. *Anthurium subovatum* Matuda, *Croat 48066.*—199. *Anthurium testaceum* Croat & Baker, *Croat 26646.*

3.6 mm long, ca. 1.6 mm wide with minute, triangular appendage at base. Figs. 186 and 197.

Anthurium spectabile occurs in Costa Rica at 500 to 900 m in premontane wet forest and tropical wet forest.

The species is recognized by its elongate, pendent leaf blades with numerous, prominent, primary lateral veins supported on an erect, 4-sided petiole. Also distinctive is the inflorescence with its short peduncle, large, narrowly ovate, often violet-purple spathe and yellow spadix. *Anthurium spectabile* has been placed in section *Pachyneurium.*

Anthurium spectabile is easily confused with *A. ranchoanum,* which has similar leaves (especially on dried herbarium material) and a similar inflorescence. *Anthurium ranchoanum,* however, has a subterete petiole and a leaf blade held more or less erect or in line with the petiole. *Anthurium spectabile* also has an elongate, more or less spreading spathe, while the spathe of *A. ranchoanum* is shorter and usually stiffly erect.

Anthurium spectabile is also similar to *A. pseudospectabile* (Croat ined.) from Panama, but the latter has longer blades with more undulate margins, terete petioles, and occurs in premontane rain forest.

COSTA RICA. ALAJUELA: Cariblanco, *Lent 3543* (F); NE of Villa Quesada, *Croat 46968* (MO); *Molina et al. 17287* (F). LIMÓN: Guápiles, *Smith 4982* (US); S of Siguirres, *Croat 43325* (MO).

Anthurium standleyi Croat & Baker, Brenesia 16 (Supl. 1): 88. 1979. TYPE: Costa Rica. San José: ca. 5 miles SW of Canaán along gravel road from Rivas; steep slopes, ca. 900 m elev. 14 August 1977, *Croat 43439* (MO-2582987, holotype; CR, F, K, NY, PMA, SEL, US, VEN, isotypes; Live at MO).

Terrestrial, ca. 1.75 m tall; stems to 90 cm long, 3–5 cm diam.; internodes ca. 1 cm long; leaf scars 2–3 cm wide; roots dense, tan, fuzzy, descending, ca. 1.2 cm thick at stem, tapering slightly; cataphylls curled into a tubular cylinder, 15–30 cm long, somewhat coriaceous, short-acuminate and apiculate at apex, the apiculum ca. 1.5 cm below apex of cataphyll, drying tan (B & K Red 9/10), weathering into long, subpersistent fibers. LEAVES with petioles erect to spreading, 43–120 cm long, 7–16 mm diam., terete; geniculum 2–4.5 cm long; blades ovate, moderately thin, obtuse to usually short-acuminate at apex, lobed at base, 40–75 cm long, 25–56 cm wide, broadest at point of petiole attachment or slightly above; anterior lobe 33–55 cm long, the margins broadly convex; posterior lobes 8–21 cm long; sinus spathulate to obovate, often overlapping, the inner edges turned up, acute at apex; upper surface semiglossy to glossy, lower surface semiglossy; midrib triangularly raised above, diminishing toward apex, convexly raised below; basal veins 4–6 pairs, 4 or 5 of them coalesced 1–4 cm, raised above and below; posterior rib slightly curved, naked, the outer margin sharp and often rolled up; primary lateral veins 5–9 per side, departing midrib at 45°–65° angle, straight then arcuate-ascending, usually only the uppermost loop-connecting, convexly raised above and below; interprimary veins obscure or occasionally raised in valleys above, raised below; secondary veins slightly sunken in posterior lobes above, flat and slightly darker than surface below; collective vein arising from one of the primary lateral veins in the upper half of the leaf, 4–11 mm from margin, slightly sunken above, raised below. INFLORESCENCE erect to spreading, much shorter than the leaves; peduncle 29–76 cm long, 4–9 mm diam., terete; spathe moderately thick, green (B & K Yellow-green 6/7.5), oblong-lanceolate, 10.5–18 cm long, 2–4 cm wide, broadest ca. 1 cm above point of attachment, narrowly acuminate at apex, obtuse to rounded at base, inserted at 60° angle on peduncle; stipe 11–70 mm long in front, 6–60 mm long in back, ca. 5 mm wide, medium green; spadix green before anthesis, soon heavily tinged with violet-purple, turning yellowish-brown, 10–30 cm long, 7–10 mm diam. at base, 4–6 mm diam. at apex; flowers rhombic to weakly 4-lobed, 3.5–3.6 mm long, 2.9–3.3 mm wide, the sides nearly straight parallel to spirals, smoothly sigmoid perpendicular to spirals; 5–7 flowers visible in the principal spiral, 5–10 flowers visible in the alternate spiral; tepals semiglossy, smooth, with numerous nectar droplets, lateral tepals 1.9–2 mm wide, the inner margin broadly rounded; pistil weakly raised, medium green; the stigma linear, 0.4–0.7 mm long, a slight slit briefly filling with nectar a few days before first stamens appear, dry and slightly darkened when stamens emerge; stamens beginning to emerge from or near the base, all 4 stamens in a spiral opening soon after the first, held in a close circle around pistil, obscuring pistil; anthers orange to greenish-yellow, 0.6–1 mm long, ca. 1 mm wide; thecae ellipsoid; pollen orange, fading creamy white. INFRUCTES-

CENCE arching; spathe reflexed; spadix to 30 cm long, 2 cm wide; berries broadly ovoid, rounded at apex, orange; mesocarp pulpy, bitter tasting; seeds 2, white, to 5 mm long. Figs. 188 and 189.

The species is in section *Pachyneurium* and is known for certain only from Costa Rica in the Cordillera de Talamanca. It was first collected by Paul Standley at two sites, La Verbena and San Sebastian south of San José, in what is probably premontane wet forest. It has been collected more recently in the region northeast of San Isidro del General. The species ranges from 900 to 1,900 m elevation and may be restricted to premontane wet forest.

A cultivated collection from the University of Hawaii was reportedly based on a Dressler collection from Achiote, a region of tropical moist forest in the Isthmus of Panama. The species has never been collected in Panama to our knowledge, and the collection cultivated in Hawaii is probably mislabelled.

COSTA RICA. SAN JOSÉ: Cerro Tapezco, *Jimenez 627* (US); ½ mile above turnoff to Canaán at Rivas, *Croat 43431* (MO); *43439* (CR, F, K, MO, NY, PMA, SEL, US, VEN); vicinity La Verbena, *Standley 32243* (US); vicinity San Sebastian, *Standley 49296* (US); along banks of Río Buena Vista, S of Buena Vista, NE of San Isidro del General, *Luteyn 3287* (DUKE); Río Herradura, NW of Canaán, *Burger & Liesner 7093* (MO, US); Talamanca, *Tonduz 8721* (NY).

Anthurium subcordatum Schott, Oesterr. Bot. Z. 8: 181. 1858.

a. **Anthurium subcordatum** ssp. **subcordatum.** TYPE: Guatemala. Quetzaltenango: Las Nubes on slopes of Volcán Zunil, 8,000′, *Wendland 330* (GOET).

Anthurium basiattenuatum Standl. ex Yuncker, Field Mus. Nat. Hist., Bot. Ser. 17:316, Pl. 4. 1938. TYPE: Honduras. Comayagua: ridge above El Achiote. *Yuncker et al. 6268* (F, holotype).

Anthurium coibionii Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 209. 1947. TYPE: Guatemala. Zacapa: Sierra de Las Minas, *Steyermark 42212* (F, holotype; US, isotype).

Epiphytic or terrestrial; stem thick, 1.5–4 cm diam.; leaf scars 2.5 cm wide; roots moderately thick, green, descending; cataphylls subcoriaceous, 5–11.2 cm long, narrowly rounded, apiculate at apex, drying light brown, dilacerating at base, persisting. LEAVES spreading; petioles sharply and shallowly sulcate, 16–44 cm long, 6–9 mm diam.; geniculum 1.5–2.2 cm long; blades ovate to narrowly triangular, moderately thick, gradually acuminate at apex, rounded, truncate or shallowly lobed at base, 28–62 cm long, 10.5–25 cm wide, broadest well above base; anterior lobe 28–40 cm long, the margins ± straight; posterior lobes 4–8 cm long; sinus arcuate, to parabolic, rarely hippocrepiform, rounded at apex; both surfaces semiglossy, the lower surface sometimes glaucous; the midrib convexly raised above and below, sunken toward apex above; basal veins 2–3 pairs, usually free to base; posterior ribs naked, the outer margins weakly rolled up; primary lateral veins 6–9 per side, departing midrib at 40°–70° angle, sunken above; intermediate and secondary veins sunken above; tertiary veins conspicuous below, flat; collective arising from the first basal vein, 6–11 mm from margin. INFLORESCENCE erect-spreading, shorter than leaves; peduncle 10–38 cm long, 2–4.5 mm diam., terete, sometimes tinged violet-purple; spathe thin, green sometimes suffused with violet-purple (B & K Yellow-green 7/10), lanceolate to narrowly ovate, 2.5–7.6 cm long, 1.4–2.7 cm wide, abruptly acuminate at apex, truncate to rounded at base, inserted at 30° angle on peduncle; stipe to 17 mm; spadix dark violet-purple or green heavily tinged violet-purple, 3.5–13.5 cm long, 5.5–9 mm diam. at base, 3–6 mm diam. at apex; flowers rhombic to sub-4-lobed, 2.5–3.5 mm long, 3–3.5 mm wide, the sides straight to sigmoid, difficult to discern; 5–7 flowers visible in the principal spiral, 8–11 flowers visible in the alternate spiral; tepals matte to semiglossy, minutely papillate, lateral tepals 1.3–1.8 mm wide, the inner margins ± straight; pistils emergent, green; stigma oblong-elliptic to linear, 0.4–0.9 mm long; stamens emerging in a moderately rapid sequence from the base, the laterals emerged from one fifth to two thirds the length of spadix before third to fourth emerge at base, held above and obscuring pistil then retracting and opening; anthers tan or orange-brown, 1 mm long, 0.8–12 mm wide; thecae oblong-ellipsoid, scarcely divaricate; pollen cream to yellow. INFRUCTESCENCE erect to spreading; berries obovoid, red, ca. 1 cm long, 1.2 cm wide; seeds 2, ca. 6 mm long, 5.5 mm wide. Figs. 191 and 196.

The species ranges from western Guatemala in the Departments of Huehuetenango, Quiché and Alta Verapaz to northern El Salvador and western Honduras at elevations from 1,100 to

2,800 m. The species occurs in moist and wet forest.

Anthurium subcordatum is in section *Belolonchium* and, like a number of Mexican and Central American species, is quite variable, characterized by its thick, truncate to subcordate leaf blades, sharply sulcate petioles, violet-purple spadix (or sometimes green heavily tinged violet-purple), and bright red, ovoid berries. The species is probably most closely related to *A. subovatum* from the Sierra de Juárez in northern Oaxaca (Mexico) but differs in having the blade generally broadest well above the base (even on cordate blades as the posterior lobes are turned inward) with most of the tertiary veins obscure, in having the basal veins usually fewer in number (1–3) and usually widespread, sometimes having the second basal vein running to the apex or to the margin well above the middle. *Anthurium subovatum* has 3–4 basal veins, usually tinged with red and these are generally directed toward the apex at a more acute angle than those of *A. subcordatum.* In addition, the berries of *A. subcordatum* are bright red whereas those of *A. subovatum* are orange. In his discussion of *A. subcordatum* in *Flora of Guatemala,* Steyermark (Standley & Steyermark, 1958) referred to *A. quinquinervium* Kunth of South America as a close relative and believed that the two species might be synonymous. Although I have not seen live material of the latter species, it is unlikely that the two are synonymous.

Anthurium subcordatum consists of two subspecies. Subspecies *subcordatum* extends throughout the range of the species. Subspecies *chlorocardium* is endemic to the slopes of Cerro Santa Bárbara (Dept. of Santa Bárbara) in western Honduras.

Populations of *A. subcordatum* from southwestern Honduras were described as *A. basiattenuatum* by Standley based on the more acute leaf base, but they are well within the expected range of variation of ssp. *subcordatum* and are connected to the more typical populations from El Salvador and Guatemala by another Honduran collection (*Molina 22322*).

It is somewhat unusual that both extremes of the leaf shape variation occur in Honduras since ssp. *chlorocardium* is at the opposite extreme from *A. basiattenuatum,* with well developed posterior lobes.

EL SALVADOR. CHALATENANGO: E slope of Los Esesmiles, *Tucker 1048* (F, UC, US). SANTA ANA: Cerro Montecristo, *Molina et al. 16836, 16914* (F, NY, US); *Wilbur et al. 16358* (DUKE, MO); *Croat 42395, 42396, 42500* (MO); *Molina & Molina 12680* (F); Cerro Miramundo, *Carlson 940* (F).

GUATEMALA. ALTA VERAPAZ: W of San Cristóbal, *Standley 89750* (F); San Juan Chamelco, *Wilson 40926* (F). CHIQUIMULA: near Village of El Brujo, *Steyermark 30935* (F). EL PROGRESSO: Sierra de las Minas, N of Finca Piamonte, *Steyermark 43608* (F, NY, US). HUEHUETENANGO: San Juan Ixcoy, *Steyermark 50017* (F); *50041* (F, NY); San Mateo Ixtatán, *Breedlove 8786* (DS, F, US); Sierra de los Cuchumantes, Cerro Cananá, *Steyermark 49109* (F, US). JALAPA: between Jalapa and Lake Ayarza, *Steyermark 32814* (F). QUEZALTENANGO: vicinity Quezaltenango, *Standley 86557* (F). QUICHÉ: no other location, *Aguilar 1276* (F); *Hyde & Lux 3516* (GH, K, US); Nebaj, *Skutch 1697* (F, GH). ZACAPA: Río Sitio Nuevo, near Santa Rosalía, *Steyermark 42212* (F, US); Sierra de Las Minas, *Steyermark 29877, 42541* (F).

HONDURAS. COMAYAGUA: El Achiote, *Yuncker et al. 6268* (F, GH, MICH, MO); *6272* (F, GH, MO). OCOTEPEQUE: vicinity Nueva Ocotepeque, *Molina 22322* (F).

b. Anthurium subcordatum ssp. **chlorocardium** (Standl. & L. O. Wms.) Croat, comb. nov. *A. chlorocardium* Standl. & L. O. Wms., Ceiba 3: 103. 1952. TYPE: Honduras. Santa Bárbara: upper rocky slopes and summit of Cerro Santa Bárbara, alt. 2,750 m, April 5–6, 1951, *Allen et al. 6075* (US, F).

Epiphyte; cataphylls 6–10 cm long, weathering to longitudinal fibers. LEAVES with petioles 27–44 cm long, 6–8 mm diam.; blades ovate, moderately thick, 26–37 cm long, 18–24 cm wide, broadest just below middle, acute at apex, lobed at base; the anterior lobe 24–29 cm long; posterior lobes 6.5–8 cm long; the sinus parabolic, round at apex; the midrib drying ± flat above, raised below; basal veins 3–5 pairs; primary lateral veins 6–8 per side, drying raised on both surfaces; lesser veins drying prominulous on both surfaces; collective vein arising from the first or second basal vein. INFLORESCENCE with peduncle 13.5–39.5 cm long, 4–5 mm diam.; spathe green, thick, 5–12 cm long, 1.5–6.5 cm wide, narrowly ovate to ovate, long-acuminate at apex, cordate at base, broadest just above base; spadix 4–12 cm long, 1.5–2 cm diam.; flowers rhombic, 5–6 mm long; 4.5–6 mm wide, 6–7 flowers visible in the principal spiral, 6–8 flowers visible in the alternate spiral; lateral tepals 1.5–1.8 mm wide; pistils raised; stigmas linear, ca. 0.6 mm long, drying brown; stamens exserted on filaments ca. 0.5 mm long, ca. 0.9 mm wide; thecae ellipsoid. INFRUCTESCENCE with subglobose

berries, ca. 6 mm diam., immature berries yellow. Fig. 190.

Anthurium subcordatum ssp. *chlorocardium* is endemic to Honduras on Cerro Santa Bárbara (Department of Santa Bárbara) at elevations of 2,200 to 2,750 m.

Subspecies *chlorocardium* is a member of section *Belolonchium* and is distinguished by its narrowly ovate to ovate spathe and its geographical isolation.

HONDURAS. SANTA BÁRBARA: summit of Cerro Santa Bárbara, *Allen et al. 6075* (F, US); E of Lake Yojoa, *Clewell & Hazlett 3916* (MO, US).

Anthurium subovatum Matuda, Bol. Soc. Bot. México 24: 36. 1959. TYPE: Mexico. Oaxaca: road between Cerro Pelón and Yetla, elev. 1,900 m, January 12, 1959, *MacDougall 406* (MEXU, holotype).

Terrestrial or epiphytic; stem to 2.5 cm diam.; leaf scars ca. 2.3 cm wide; roots tan, numerous, 3–8 mm diam.; cataphylls moderately thick, 5–8.5 cm long, acute at apex, subapical apiculum 1.9–2.7 cm long, drying brown, persistent, splitting at base, remaining intact at apex. LEAVES with petioles erect-spreading, 20–51 cm long, 5–7 mm diam., shallowly and broadly sulcate, the margins sharp, rounded abaxially; geniculum 1–2 cm long, usually tinged red-violet; blade narrowly ovate-triangular to ovate, moderately thick, acute and apiculate at apex (acumen 2–5 mm long), weakly to prominently lobed at base, 27–44 cm long, 10–26 cm wide, broadest at base or just above point of petiole attachment; anterior lobe 26–41 cm long, the margins ± straight to convex; posterior lobe 4.5–13 cm long, usually directed upward from point of petiole attachment; sinus arcuate with petiole decurrent to arcuate to parabolic (when flattened), round to truncate at apex; upper surface semiglossy, lower surface matte, both surfaces sometimes glaucous; midrib weakly, convexly raised above, broad at base, narrowing and sunken at apex, convexly raised almost to apex below; basal veins 3–5 pairs, the first free, second to fifth coalesced 1–3 cm; posterior rib naked; primary lateral veins 3–7 per side, departing midrib at 30°–50° angle, loop-connecting to collective vein, sunken above, raised below; secondary and tertiary veins clearly visible, weakly sunken above, raised below; midrib, basal, and primary lateral veins usually tinged red-violet on lower surface, sometimes faintly tinged on upper surface; collective vein usually arising from the first or second basal vein, sunken above, raised below, 4–7 mm from the margin. INFLORESCENCE spreading to pendent, ca. as long as leaves; peduncle 28–49 cm long, 4–6 mm diam., sometimes weakly glaucous or tinged red-violet; spathe moderately thick, lanceolate, green sometimes suffused with red-violet, matte on both surfaces, 6–9.5 cm long, 1.5–2.7 cm wide, gradually acuminate at apex, rounded to obtuse at base, inserted at 40°–50° angle on peduncle; spadix green turning dark violet-purple, 10.3–19 cm long, 7–11 mm diam. at base, 3–4 mm diam. at apex; flowers rhombic to 4-lobed, 3.7–4.2 mm long, 3.2–3.9 mm wide, the sides weakly to jaggedly sigmoid; 5–7 flowers visible in the principal spiral, 6–12 flowers visible in the alternate spiral; tepals matte, minutely punctate, with sparse droplets as stamens emerge, lateral tepals 1.5–2.6 mm wide, the inner margin broadly rounded, usually turned up against pistil; pistil green, tinged violet-purple, weakly emergent; stigma linear, ca. 0.8 mm long; lateral stamens emerging slowly from the base, one at a time, the alternates following by 1–3 spirals; faint yeasty odor as stamens emerge; anthers creamy white, held in tight circle, retracting slightly as pollen disperses; thecae ovoid; pollen pale yellow to creamy white. INFRUCTESCENCE spreading-pendent; spathe green, persistent; berries bright orange, sometimes developing only in the basal one half, broadly obovate, rounded to truncate at apex, 6–9 mm long, 7–9 mm wide; mesocarp thick, juicy with numerous raphide cells; seeds 1 or 2, pale green, obovoid-ellipsoid, weakly flattened, 4.5–5.6 mm long, 3.5–5 mm wide, 2.8–3 mm thick, with sticky appendages at both ends. Figs. 192 and 198.

Anthurium subovatum is restricted to Mexico in the Sierra de Juárez of northern Oaxaca at 1,500 to 2,100 m in cloud forests in what appears to be a premontane rain forest life zone.

The species is a member of section *Belolonchium* and is characterized by its sharply sulcate petioles, thick subcordate to truncate leaf blades with sharply ascending reddish basal veins, numerous clearly visible tertiary veins, violet-purple spadix, and obovoid, more or less truncate, bright orange berries. It is similar to *A. subcordatum* in having a similar leaf shape, but the blades of *A. subovatum* are generally broadest at the base with the posterior lobes often directed

somewhat upward on well developed plants. *Anthurium subovatum* also generally has the spadix sessile or nearly so and has orange berries, whereas the spadix of *A. subcordatum* is often conspicuously stipitate and the berries are red. For additional characters see the discussion following *A. subcordatum.*

Anthurium subovatum is also similar to *A. nakamurae,* a species apparently endemic to eastern Chiapas. That species differs in having blades more typically oblong and usually broader toward the apex. Considering the variability in *Anthurium* it is possible that *A. subcordatum, A. subovatum* and *A. nakamurae* may ultimately be proven to be no more than subspecifically distinct.

MEXICO. OAXACA: highway between Cerro Pelón and Yetla, *MacDougall 406* (MEXU); N of Ixtlán de Juárez on the road to Tuxtepec, *Rzedowski 30615* (MO); along road between Valle Nacional and Oaxaca, *McAlpin 1047* (DUKE); between Tuxtepec and Oaxaca at Valle Nacional, *Croat 39815, 39847, 48066, 48082* (MO); S of Valle Nacional, *Rzedowski 33574* (ENCB).

Anthurium subsignatum Schott, Bonplandia 9: 368. 1862. TYPE: Costa Rica. Limón: Pedregal, *Wendland 919* (GOET).

Epiphytic creeper; stems green, 10 cm or more long; internodes 1.5–11 cm long; roots pale green, 2–4 mm diam.; cataphylls subcoriaceous, 3.5–10 cm long, rounded at apex, with thick subapical apiculum ca. 4 mm long, drying reddish brown, weathering into longitudinal fibers, persisting at nodes. LEAVES with petioles spreading, 14.5–56 cm long, 3–7 mm diam., terete, sometimes sharply and narrowly sulcate; geniculum 1.5–3 cm long, obscurely sulcate, blades ovate-deltoid, short-acuminate at apex, broadly lobed to arcuate at base, 16–48 cm long, 11–52 cm wide, broadest at base; the anterior lobe 13.5–38 cm long, the margins ± straight to convex; posterior lobes 4–21 cm long; sinus arcuate to parabolic, obtuse to rounded at apex; upper surface matte to semiglossy, lower surface semiglossy; the midrib convexly to ± acutely raised above, diminished and sunken at apex, acutely raised below; basal veins 3–5 pairs, the first usually free, the remaining coalesced 2–5 cm; posterior rib naked, weakly turned up; primary lateral veins 4–9 per side, weakly sunken above, prominulous below, loop-connecting; lesser veins less conspicuous; collective vein usually arising from the first basal vein, rarely from one of the lowermost primary lateral veins, sunken above, prominulous below, 3–5 mm from margin. INFLORESCENCE erect, shorter than leaves; the peduncle 7.5–28 cm long, 3–6 mm diam.; spathe moderately thin, yellow-green, oblong-lanceolate, 5–25 cm long, 1.3–4 cm wide, long-acuminate at apex, truncate at base, inserted at 45° angle on peduncle; spadix yellow to yellow-green, 5.5–26 cm long, 6–9 mm diam. at base, 3–5 mm diam. at apex; flowers 4-lobed, ca. 2 mm long, 2.2 mm wide, the sides jaggedly sigmoid; 4–7 flowers visible in the principal spiral, ca. 9 flowers visible in the alternate spiral; tepals glossy, lateral tepals ca. 1 mm wide, the inner margin convex; pistil minutely emergent, white, glossy; stigma ca. 2 mm long, brushlike, with very small droplets for 5–6 days about 7–8 days before first stamens emerge, dry, white to tan when stamens emerge; stamens emerging from base in moderately rapid sequence, the second lateral stamen emerging 1 or 2 days after first stamen; anthers yellow-orange; pollen pale yellow-orange. INFRUCTESCENCE with spadix to 30 cm long; berries obovoid, violet-purple at apex, white at base, acute at apex, ca. 5 mm long; seeds 1–2, white, 1.5 mm long. Figs. 193 and 194.

Anthurium subsignatum is endemic to northern Costa Rica at sea level to 200 m elevation in tropical wet and premontane wet forest life zones.

This species is a member of section *Semaeophyllium* and was mistakenly included as a synonym of *A. trilobum* André in "*Anthurium* in Costa Rica" (Croat & Baker, 1979). It is closely related to *A. garagaranum* Standl. of Panama and Colombia, which has a similar bright yellow spadix at anthesis. The latter species differs in having more deeply lobed leaf blades. Madison (1978) included *A. garagaranum* as a synonym of *A. trilobum* with admitted misgivings, but additional field work is needed in South America to make an analysis of this complex.

COSTA RICA. ALAJUELA: Cañas-Upala road, N of Bijagua, *Croat 36429, 36455, 36485* (MO). HEREDIA: Chilamate, *Leon 1784* (US); La Selva Field Station, *Grove 34* (MO); *Croat 44234* (MO); near Puerto Viejo along road near Río Sucio, *Croat 35748* (MO). LIMÓN: vicinity Guapiles, *Standley 37458* (US); Hacienda Tapezco-Hda. La Suerte, W of Tortuguero, *Davidson & Donahue 8366, 8654* (MO).

Anthurium tenerum Engl., Bot. Jahrb. Syst. 25: 377. 1898. TYPE: Colombia. Antioquia: Cerro El Plateado in western Andes, dense humid forest, 1,800–2,200 m, *Lehmann 7354* (B, K).

Scandent epiphyte; stems elongate with internodes 1.5–7.5 cm long; roots moderately thin, usually 2–4 at each node; cataphylls 4–6 cm long, thin, acute at apex, drying tan, persisting intact at nodes. LEAVES spreading; petioles 1–3 cm long, 2–3 mm diam., terete, sheath extending 1.5–2 cm onto petiole, minutely free at apex; geniculum absent; blades oblong or lanceolate, moderately thin, 9–15 cm long, 2.5–4 cm wide, broadest at middle or just below, acuminate at apex, obtuse to rounded at base; the upper surface semiglossy to glossy, lower surface semiglossy; midrib acutely raised above and below, sunken at apex above; primary lateral veins numerous, nearly obscure above and below; collective vein arising from the base, obscure above and below. INFLORESCENCE spreading, shorter than leaves; peduncle 2.5–4 cm long; spathe green, ovate, 1.5–2 cm long, 2–9 mm wide; spadix green (B & K Yellow-green 6/2.5), ca. 3 cm long, scarcely tapered at apex; flowers 4-lobed, the sides sigmoid; 4–5 flowers visible in the principal spiral, 3–4 flowers visible in the alternate spiral; tepals semiglossy, punctate, the inner margin convex; pistils green, emergent, ± mounded; stigma elliptic, brushlike. INFRUCTESCENCE pendent; spathe absent; spadix to 3.5 cm long; berries subglobose flat at apex, greenish-white immature, mature berry color unknown, probably 5 mm diam. at maturity. Fig. 195.

Anthurium tenerum is known from Costa Rica and Colombia (probably in Panama as well) at elevations of 800 to 2,000 m. In Costa Rica the species is known from lower montane rain forest at 1,300 m. It is apparently also rare in Colombia since few collections have been made.

The species is in section *Xialophyllium* and is most easily confused with *A. scandens* because of its similar habit, size, and leaf shape. *Anthurium tenerum* can be distinguished by its lack of leaf punctations and by its long slender peduncle which is, at least initially, borne in the conspicuous petiole sheath.

COSTA RICA. CARTAGO: vicinity of Cachí, *Croat 47089* (MO); vicinity Río Naranjo, *Lent 1583* (NY). HEREDIA: Vara Blanca, *Skutch 3658* (MICH).

Anthurium testaceum Croat & Baker, Brenesia 16 (Supl. 1): 92. 1979. TYPE: Costa Rica. Alajuela: Atlantic side of Alto de las Palomas, 1,900 m, *Lent 1820* (F, holotype).

Epiphytic or terrestrial; stems elongate, ca. 1 m long, 1–1.5 cm diam., drying irregularly grooved on 1 or more sides; internodes 1.5–2.5 cm long; leaf scars moderately inconspicuous, ca. 1 cm wide; roots few, scattered at the nodes; cataphylls moderately thin, 6–15 cm long, green, sometimes tinged purplish, apiculate at apex, drying greenish-yellow to brown, dilacerating and often persisting, ultimately deciduous. LEAVES spreading, scattered in upper part of stem; petioles (8)14–48 cm long, 3–6 mm diam., terete; geniculum 5–15 mm long; blades oblong-lanceolate to lanceolate or oblong-elliptic, moderately thin, gradually acuminate to cuspidate-acuminate at apex (the acumen 1–3 cm long), obtuse to rounded (rarely acute) at base, 18–50 cm long, 4–12.5 cm wide, broadest usually below the middle, the margin ± straight; upper surface matte to semiglossy, lower surface matte; midrib weakly raised in a valley above, prominently raised below; primary lateral veins 10–16 per side, departing midrib at 60°–80° angle, weakly sunken above, raised below, loop-connecting to collective vein; lesser veins obscure; collective vein usually arising from the first to third primary lateral vein, 1–8 mm from margin. INFLORESCENCE spreading, usually shorter than leaves; peduncle 14–40 cm long, 3–5 mm diam., terete, three quarters to equally as long as petioles; spathe ± thin, green, lanceolate, 3–7 cm long, 7–14 mm wide, acuminate at apex, slightly clasping and rounded at base; spreading, inserted at 60° angle on peduncle; stipe 2–8 mm long in front, 1–7 mm long in back, ca. 3 mm diam.; spadix green, sometimes tinged with violet-purple, 4–12 cm long, 4–6 mm diam. at base, 2–4 mm diam. at apex; flowers rhombic, 1.8–4 mm long, 1.5–3 mm wide, the sides straight to slightly jaggedly sigmoid; 2–4 flowers visible in either spiral; tepals matte to semiglossy, densely and minutely papillate, turned up against the emerging pistils, lateral tepals 1.8–5 mm wide, inner margin convex, thin, pale, the alternate pair with inner margins convex; pistils early emergent, green; stigma ca. 0.5 mm long, elliptic; stamens held at or above the tepals on translucent filaments 0.5 mm long, 0.3 mm wide, lateral stamens developing throughout, followed quickly by alternates; anthers orange, 0.5–0.8 mm long, ca. 1 mm wide; thecae ellipsoid, slightly divaricate; pollen orange fading to yellow. INFRUCTESCENCE with spadix 7–14 cm long; berries oblong-ellipsoid, rounded at apex, bright red, 9–13 mm long, 5–7 mm diam., prominently exserted before maturity, mesocarp gelatinous; seeds 2, oblong-ellipsoid to elliptic, rounded at both

ends, tan, scarcely flattened, 3–7 mm long, 3–4 mm wide, 2.5–3.4 mm thick, an appendage enveloping the seed, extending beyond both ends and at least one side. Fig. 199.

The species is found in Costa Rica and Panama at 800 to 2,000 m elevation in premontane wet and premontane rain forest life zones. In Costa Rica the species ranges from Monteverde in Puntarenas and Alajuela Provinces to San Vito de Java near the Panamanian border. In Panama the species is known only from western Panama near Costa Rica.

Anthurium testaceum can be distinguished by its elongate, narrow stem, long, thin, persistent cataphylls, bright red, prematurely exserted berries, few-flowered spadix spirals, and lanceolate leaf with the midrib and primary lateral veins drying very pale tan.

The species is probably closest to *A. cerropirrense* Croat (ined.) from Darién Province in eastern Panama, but that species differs in having 5–7 flowers per spiral and tepals that are not at all elevated. It also has shorter internodes and purple berries.

Live material of this species has been confused with specimens of *A. pallens. Anthurium pallens* differs, however, by its smaller, yellow berries, the midrib and primary lateral veins not significantly different in color from the blade, and the secondary veins more numerous and prominent than in *A. testaceum*. The veins of *A. testaceum* probably appear more striking because of the great contrast between the rich green lower leaf surface and the light, almost bleached appearance of the veins. In "*Anthurium* in Costa Rica" (Croat & Baker, 1979) it was suggested that it would best be placed in section *Leptanthurium*; it is, however, best placed in section *Xialophyllum*.

COSTA RICA. Junction of Alajuela, Guanacaste, Puntarenas, *Burger et al. 10840* (MO). PUNTARENAS: along Río Coto Brus, near Cotán, N of La Unión, *Croat 26646* (MO). SAN JOSÉ: above Río Cascajal, *Lent 4040* (MO).

Anthurium tilaranense Standl., J. Wash. Acad. Sci. 17: 245. 1927. TYPE: Costa Rica. Guanacaste: Quebrada Serena, southeast of Tilarán, 700 m, Jan. 1926, *Standley & Valerio 46310* (US, holotype).

Anthurium latihastatum Engl. ex K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11: 612. 1932. SYNTYPES: Costa Rica. near San Ramón, 1,300–1,400 m, May 1913, *Tonduz 17708* (not seen); near San Ramón, 1,200 m, *Tonduz 17704* (not seen).

Epiphyte; stems to 1 m long; internodes short; cataphylls 7–17 cm long, round at apex with subapical apiculum, drying reddish-brown (B & K Yellow-red 7/10), persisting intact. LEAVES with petioles spreading, (8)16–45 cm long, 4–6 mm diam.; blades subcoriaceous, 3-lobed, 20–46 cm long, 10–60 cm wide; the median lobe oblong, acuminate at apex, the lateral lobes falcate, the inner margin concave, the outer margin convex; the lateral lobes 5.5–15 cm long; the median lobe 17–24 cm long, the margins straight, shallowly lobed at base; sinus usually arcuate, usually rounded to truncate at apex; both surfaces semiglossy; midrib of the median lobe convexly raised to just below middle, diminished and sunken at apex above, prominently and acutely raised below; basal veins 1–3 pairs, 2 of them coalesced to 4 cm; posterior ribs submarginal, prominently raised; primary lateral veins 7–10 per side, departing midrib at 40°–60° angle, flat above, ± obscure below, straight or curving near collective vein; lesser veins obscure; collective vein arising from second basal vein and extending along outer edge of posterior lobes to the apex of the median lobe, 3–4 mm from the margin. INFLORESCENCE ± erect, shorter than leaves; peduncle (7)10–25(30) cm long; spathe subcoriaceous, pale green, broadly lanceolate to oblong or oblong-elliptic, 5.5–11 cm long, 1.7–3 cm wide, abruptly acuminate at apex, acute at base; spadix pale green to white (B & K Yellow-green 8/10), 4.5–14 cm long, ca. 8 mm diam. midway; flowers rhombic to sub-4-lobed, 2.4–2.8 mm long, 2.8–3.3 mm wide, the sides straight to jaggedly sigmoid; 7–8 flowers visible in the principal spiral and 5–7 flowers visible in the alternate spiral; tepals smooth, glossy, the lateral tepals 1.4–1.5 mm wide, the inner margin obtusely angular, the outer margin 5-sided; pistils weakly emergent ca. 0.3 mm; stigma round, 0.2 mm diam., brushlike; stamens emerging in a rapid progression beginning in the apical half of spadix, the laterals exserted throughout before the alternates emerge, scarcely exserted above tepals on fleshy filaments; anthers white, ca. 0.3 mm long, 0.5 mm wide, held close but not contiguous; thecae ovate-ellipsoid, slightly divaricate; pollen white. INFRUCTESCENCE with spadix to 22 cm long; berries red (at least apically), obovoid, ca. 7 mm

FIGURES 200–203. 200. *Anthurium tilaranense* Standl., *Croat 36318*.—201–202. *Anthurium tonduzii* Engl., *Croat 37247*.—203. *Anthurium trinerve* Miq., *Croat 36357*.

long, 5 mm diam., obtuse at apex; mesocarp clear, gelatinous; seeds 2, greenish, ca. 3.5 mm long, 2.5 mm wide, 1.5 mm thick. Fig. 200.

The species is known from Costa Rica and Panama at 400 to 1,500 m elevation in premontane wet, tropical wet, and lower montane forest. It is a member of section *Semaeophyllium* and is not close to any other species in the section. It is distinguished by its deeply 3-lobed leaf blade, with the lateral lobes falcate, persistent cataphylls, and pale green to white spadix that is slightly tapered at both ends. In Costa Rica it can be confused only with *A. subsignatum*, which has blades only weakly 3-lobed and a bright yellow spadix. In Panama it has leaves similar to *A. madisonianum* Croat (ined.), which has a longer, reddish-violet spadix and prominently dilacerated cataphylls.

COSTA RICA. ALAJUELA: Cañas-Upala Road, NNE of Bijagua, *Croat 36257, 36318* (MO); between Naranjo and Quesada, N of Zapote, *Croat 46922* (MO); N of Río Naranjo on road to Upala, *Utley & Utley 4039* (DUKE, MO). CARTAGO: vicinity Moravia, *Croat 36685* (MO); between Las Vueltas de Tucurrique and El Oriente, *Bogner s.n.* (MO). GUANACASTE: Los Ayotes near Tilarán, *Standley & Valerio 45586* (US); slopes of Volcán Miravalles, *Luteyn 3409* (DUKE). HEREDIA; vicinity of Vara Blanca, *Skutch 3735* (MICH). PUNTARENAS: Monteverde, *Jiménez s.n.* (MO).

Anthurium titanium Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 211. 1947. TYPE: Guatemala. San Marcos: south facing slopes of Volcán Tajumulco, above Finca El Porvenir, along Río Cabuz to within 2 mi of Cueva de las Palomas, alt. 1,300–1,500 m, March 16, 1940, *Steyermark 37963* (F, holotype).

Anthurium xanthosomifolium Matuda, Revista Soc. Mex. Hist. Nat. 11: 92. 1950. TYPE: Mexico. Chiapas: Municipio Siltepec, Cascada, on wet rock at 1,800 m, April 11, 1949, *Matuda 18644* (MEXU, holotype; DS, isotype).

Epipetric or terrestrial; stems short, 2–4 cm diam.; leaf scars 2.5–2.8 cm wide; roots thick, tan, 5–6 mm diam.; cataphylls subcoriaceous, 4.5–12 cm long, round to weakly emarginate at apex with a conspicuous subapical apiculum ca. 2 mm long, drying medium brown (B & K Yellow 4/7.5), weathering into coarse fibers. LEAVES with petioles erect-spreading, 31–90(112) cm long, 5–10(15) mm diam., D-shaped, sometimes weakly sulcate and glaucous; geniculum 1.5–4 cm long; blades moderately thick, ovate to broadly ovate or nearly round, abruptly to gradually acuminate at apex (the acumen apiculate 2–7 mm long), deeply lobed at base, 27–120 cm long, 29–80 cm wide, broadest at middle or just below, the margins sometimes markedly undulate, weakly revolute; anterior lobe 19–100 cm long, the margins broadly rounded; posterior lobes 10–40 cm long; sinus obovate to hippocrepiform, acute to rounded at apex; both surfaces semiglossy; midrib convexly raised above, more acutely raised below, narrowing and diminishing, ± flat at apex above; basal veins 7–10 pairs, the first and second free to base, those remaining coalesced 2–4(7) cm, raised above and below; posterior ribs conspicuously upturned, naked; primary lateral veins 3–5 per side, departing midrib at 45° angle, ± straight to collective vein, loop-connecting to collective vein, weakly raised above and below; interprimary veins conspicuous, flat above and below, lesser veins visible; collective vein arising from the first basal vein in smaller blades or one of the primary lateral veins in the larger blades, weakly sunken above, raised below, 7–15 mm from margin. INFLORESCENCE erect-spreading, as long as or shorter than leaves; peduncle 26–47 cm long, 7–15 mm diam., terete; spathe subcoriaceous, green, faintly to heavily tinged red-violet, broadly lanceolate, (5)9–26 cm long, 1.8–3.2 cm wide, broadest just above base, long-acuminate at apex, inrolled 1–2.5 cm, rounded at base, inserted at 25°–30° angle on peduncle, held at ca. 45° angle from peduncle; stipe 5.5–9 mm long in front, 4.5–7 mm long in back; spadix olive-green (B & K Yellow-green 5/5), sometimes weakly to heavily tinged red-violet, (6)11–24 cm long, 1–3 cm diam. at base, 5–10 mm diam. at apex; flowers rhombic to sub-4-lobed, 3.7–5 mm long, 3.8–4 mm wide, the sides ± straight to weakly sigmoid; 7–10 flowers visible in the principal spiral, 6–13 flowers visible in the alternate spiral; tepals matte, minutely papillate, lateral tepals 1.8–2.9 mm wide, the inner margin broadly rounded, thin, paler green; pistil green, emergent, raised; stigma linear, 0.7 mm long, ca. as long as pistil; stamens emerging at base, 3 or 4 stamens emerging in the first 2–3 spirals before first emerges in next spiral, held over pistil, retracting to edge of tepals before opening; filaments weakly exserted, translucent, as wide as anthers; anthers pale yellow, 0.9–1.2 mm long, 1.2–1.4 mm wide; thecae ellipsoid,

FIGURES 204–207. 204–205. *Anthurium titanium* Standl. & Steyerm., *Croat 47253*.—206. *Anthurium trinerve* Miq., *Croat 34371*.—207. *Anthurium trisectum* Sodiro, *Croat 25633*.

scarcely divaricate; pollen cream. INFRUCTESCENCE probably with orange berries. Figs. 204 and 205.

Anthurium titanium is endemic to a small area in southeastern Chiapas in Mexico and adjacent western Guatemala in the Department of San Marcos from 900 to 1,800 m, mostly from 1,300 to 1,800 m.

The species is a member of section *Belolonchium* and is characterized by its broadly ovate to subrounded blade with prominent posterior lobes and a weakly glaucous petiole, D-shaped in cross-section.

The species is probably most closely related to *A. montanum,* with which it is sympatric and shares a similar leaf texture and coloration, weathered cataphylls, and petioles that are usually D-shaped in cross-section and somewhat glaucous. The latter species differs in having a narrowly ovate blade which is generally smaller than *A. titanium.*

The type specimen is unusually large (perhaps twice as large as other collections in most aspects) but otherwise compares well with the material from Chiapas described by Matuda as *A. xanthosomifolium.* The species is by far the largest *Anthurium* in Mexico.

GUATEMALA. SAN MARCOS: La Trinidad, 2 km from Finca Armenia, *Croat 40904* (MO); Volcán Tajumulco, above Finca El Porvenir, *Steyermark 37963* (F). MEXICO. CHIAPAS: Escuintla, *Matuda 18456* (MEXU); *18628* (CAS, DS, NY); *19502* (DS, MEXU); W of Motozintla, *Croat 47253* (MO); Siltepec, *Matuda 5077* (MEXU); *18639* (NY, UC); *18644* (DS, MEXU, MO); *18799, 38603* (MEXU, MO); *19668* (MEXU, MO, NY, UC).

Anthurium tonduzii Engl., Bot. Jahrb. Syst. 25: 376. 1898. TYPE: Costa Rica. San José: near San Marcos, in forest near Alto de Pito, 1,400 m, *Tonduz 7683* (B, holotype).

Epiphytic or terrestrial, usually creeping; stems elongate, rooting at nodes; the internodes 2–21 cm long; cataphylls to 8 cm long, early deciduous. LEAVES erect-spreading; petioles subterete, narrowly and obscurely sulcate, 1.5–12 cm long, 2–3 mm diam.; geniculum 1.4–2.3 cm long; blades ovate to ovate-elliptic, moderately thick, gradually to abruptly acuminate at apex, obtuse to rounded or rarely subcordate at base, 6–13 cm long, 3.5–8.5 cm wide; both surfaces glossy, the lower surface conspicuously punctate; 1 (rarely 2) pair of basal veins, the innermost serving as the collective vein; primary lateral veins 3–6 per side, scarcely more conspicuous than the interprimary veins, sunken above, raised below; collective vein arising from the base, 4–5 mm from the margin. INFLORESCENCE erect-spreading, longer than leaves; the peduncle 3.5–14 cm long; spathe lanceolate, green tinged reddish, subcoriaceous, 1.5–3 cm long, 0.5–1 cm wide, abruptly acuminate at apex, acute at base; spadix green to red, scarcely tapered, 2.5–3 cm long, 4–5 mm diam. midway (dry); flowers rhombic to 4-lobed, ca. 2.2 mm long, 1.9 mm wide (dry), the sides straight to weakly sigmoid; 4–5 flowers visible in the principal spiral, ca. 7 flowers visible in the alternate spiral; lateral tepals 1.6 mm wide (dry), the inner margins straight to convex, pistils raised, weakly emergent; stigmas linear, 0.3–0.4 mm long; stamens emerging in a ± complete sequence from the base; anthers held in a tight cluster over pistil; thecae broadly ellipsoid. INFRUCTESCENCE with spadix to 8 cm long; berries white, turning purple at maturity, oblong, ca. 1 cm long; mesocarp clear, gelatinous; seeds 2, dark violet-purple, ca. 4 mm long, 2 mm wide and 1.5 mm thick. Figs. 201 and 202.

Anthurium tonduzii occurs in Costa Rica and Panama at 800 to 1,500 m elevation in premontane rain and lower montane rain forest. It has been collected on Cerro Pirre in Darién Province of Panama and is to be expected in Colombia in the Department of Chocó.

The type collection was made in 1893 and no collections have subsequently been made in Costa Rica but the species has been collected five times between 1975 and 1977 in Panama.

Anthurium tonduzii is in section *Tetraspermium* and does not appear to be related to any other species (certainly to no Central American species), but it looks superficially like *A. scandens* and *A. trinerve* because of similar small, punctate leaves and scandent habit. It differs from both by its longer internodes and entire deciduous cataphylls. The cataphylls of *A. scandens* and *A. trinerve* soon weather into fibers and persist, densely covering the stem.

Anthurium trinerve Miq., Linnaea 17: 67. 1843. *Anthurium scandens* var. *trinerve* (Miq.) Matuda, Anales Inst. Biol. Univ. Nac. México 15: 189. 1954. TYPE: Surinam. Palmar Awara, *Forbe 120* (U).

Anthurium brachyspathum C. Koch & Bouché in C. Koch, Allg. Gartenzeitung 25: 233. 1857. TYPE: Surinam?

Anthurium trinerve var. *obtusum* Engl., Bot. Jahrb. Syst. 25: 357–358. 1898. TYPE: Ecuador. Valle Pallatanga, *Sodiro 2* (not seen).

Anthurium trinerve var. *angustifolium* K. Krause, Bot. Jahrb. Syst. 54 (118): 123. 1916. TYPE: Bolivia. Antahuacana at Espiritu Santo, 750 m, *Buchtien* (not seen).

Anthurium codajasii G. M. Barroso, Arch. Jard. Bot. Río de Janeiro, 15: 97. 1957. TYPE: Brazil. Amazonas: Codajás, Logos de Badajós, *R. L. Froes 26590* (not seen).

Epiphyte; stems elongate, creeping, usually less than 50 cm long, 6–9 mm diam.; internodes 1–3.5 cm long; roots numerous, 2–3 mm diam., grayish-brown; cataphylls moderately thin, to 6 cm long, drying brown, weathering to longitudinal fibers and persisting around stem. LEAVES spreading; petioles 1.3–6 cm long, 2.5–3.5 mm diam., ± D-shaped, broadly and sharply sulcate; geniculum 3–5 mm long; blades moderately thick, elliptic to ovate-elliptic to lanceolate, 8–17 cm long, 3–7.5 cm wide, acute at apex, obtuse to attenuate at base; the upper surface semiglossy, lower surface glossy and conspicuously punctate; the midrib acutely raised above, convexly raised below; usually 2 pairs of basal veins, the innermost serving as a collective vein, 5–12 mm from margin in basal one quarter, closer to margin near apex; primary lateral veins numerous on each side, weakly sunken above, prominulous below; lesser veins obscure. INFLORESCENCES erect, shorter than leaves; peduncle 2–6.5 cm long; spathe thick, oblong-elliptic, greenish-white, 2.5–3.5 cm long, 0.5–1.1 (1.9) cm wide, abruptly acuminate at apex, obtuse at base, inserted at 35° angle on peduncle, held erect at anthesis; spadix dark lavender or green to white, 2–4 cm long, 5–7 mm diam. at base, 2–3 mm diam. at apex; flowers square, 2.5–4.2 mm in both directions, the sides straight to gradually sigmoid; 3–6 flowers visible in the principal spiral, 4–5 flowers visible in the alternate spiral; tepals matte to semiglossy, sometimes weakly and sparsely punctate; lateral tepals to 2 mm wide, the inner margin broadly concave; pistils emergent, white to pale green; stigma linear, ca. 4 mm long, exserted, brushlike with conspicuous stigmatic droplets 2–3 spirals ahead of emerging stamens; stamens emerging slowly from the base in a prompt and complete sequence, exserted on translucent filaments ca. 1 mm wide, 0.5 mm long; anthers white, held against pistil at same level as emerged pistil; thecae ovate-ellipsoid, widely divaricate; pollen white. INFRUCTESCENCE with spadix 4.5–6.5 cm long; berries white or sometimes pale lavender, globose, 5–7 mm diam.; seeds 4–10, oblong. Figs. 203 and 206.

The species is found in Guatemala and Belize to the Guianas and central Brazil at elevations of 0 to 800 m, in tropical moist, premontane wet, and tropical wet forest life zones. In Middle America the species has been collected only on the Atlantic slope but it occurs on both slopes in Costa Rica and Panama.

Anthurium trinerve is easily confused with *A. scandens*. It is generally found at lower elevations (to 800 m) than *A. scandens*. Other differences are discussed under *A. scandens*. It is a member of section *Tetraspermium*.

BELIZE. CAYO DISTRICT: Mountain Cow Ridge, *Gentle 3522* (MICH). STANN CREEK DISTRICT: Middlesex, *Gentle 2785, 2829* (MICH). TOLEDO DISTRICT: Temash River, *Dwyer 12841* (MO).

COSTA RICA. No other location, *Pittier 9511* (BR). ALAJUELA: Llanuras de San Carlos, *Brade 2546* (BR); Villa Quesada, San Carlos, *Smith 2528* (MO). GUANACASTE: NW of Lake Arenal, *Croat 260* (MO). LIMÓN: between Bribrí & Bratsi along Río Sixaola, *Burger et al. 10421* (MO); Limón, *Kuntze 1954* (NY). PUNTARENAS: Golfo de Nicoya, *Stork C523* (UC); Terraba, *Pittier 3865* (BR); Tinoco Station, *Allen 5472* (DS).

HONDURAS. ATLÁNTIDA: Lancetilla, *Chickering 72, 110* (MICH); *Yuncker 4557* (MO). GRACIAS A DIOS: Río Plátano behind village of Ras, *Gentry et al. 7561* (MO).

NICARAGUA. RÍO SAN JUAN: San Juan del Norte (Greytown), *Smith 35* (MO). ZELAYA: Boca Río La Tigra, Río Rama, *Stevens 8925* (MO); small Caño at Salto La Oropéndola, Río Rama, *Stevens 8964* (MO); vicinity Quebrada El Toro, along Río Iyas, *Vincelli 401* (MO); N or NW of Colonia San Antonio, *Stevens 9042* (MO); near El Recreo, *Atwood & Neill AN228* (MO); beyond Kururia on road to San Jerónimo, *Stevens 7575* (MO); road to Mina Nueva America, N of El Empalme, *Stevens 8373* (MO); road between Rosita & Puerto Cabezas, SW of Río Kukalaya, *Stevens 8507* (MO); near Río Okanwás, E of Rosita, *Neill 4476* (MO); along Río Sucio, E of Bonanza, *Neill 4027* (MO).

Anthurium trisectum Sodiro, Anales Univ. Centr. Ecuador 20: 100. 1905. TYPE: Ecuador. Esmeraldas: en la orilla del Río San Antonio, *Sodiro 8/904* (B, holotype).

Usually terrestrial, sometimes epiphytic, creeping; stems elongate; internodes 1–6 cm long; cataphylls thin, 2–9 cm long, weathering into fine longitudinal fibers, ultimately deciduous. LEAVES with petioles erect, 18–36(40) cm long, weakly sulcate; blades 3-parted, moderately thin, leaflets sessile or on petiolules to 2 cm long; median leaflet ± elliptic to ovate, 12–25 cm long, 4–11 cm wide, long-acuminate at apex, obtuse at base, lateral leaflets inequilateral ca. two-thirds

as long as median leaflet, short-acuminate at apex, inner margin attenuate at base, outer margin rounded; the midrib in the median leaflet sunken above, raised below; primary lateral veins 3–5 per side, sunken above, raised below; departing midrib at 35°–45° angle, the collective vein arising from the base, 3–5 mm from margin. INFLORESCENCE erect, shorter than leaves; peduncle 9–22 cm long, terete; spathe lanceolate or ovate, green becoming white or yellow, 4–6 cm long, 1.2–2.5 cm wide, acuminate at apex, rounded at base; spadix green to yellow, scarcely tapered, 3.7–5 cm long, 4–6 mm diam. at base; the flowers 4-lobed, ca. 1.7 mm in both directions, the sides sigmoid; ca. 6 flowers visible in the principal spiral, ca. 5 flowers visible in the alternate spiral; lateral tepals 0.9–1 mm wide, the inner margin convex; pistils emergent; stigma elliptic; stamens emerging irregularly throughout spadix, held at edge of tepals; thecae ellipsoid. INFRUCTESCENCE with spadix to 6.5 cm long, berries violet-purple, globose to ovoid, with a short beak. Figs. 207 and 208.

The species occurs from Costa Rica to Ecuador at elevations from sea level to 500 m in tropical wet forest life zones. In Costa Rica the species is known only from the OTS La Selva research area, 100 to 200 m elevation in Heredia. In Panama, the species is known only from 300 to 700 m elevation in Coclé and Veraguas Provinces, principally on the Atlantic slope.

Anthurium trisectum is in section *Dactylophyllium* and is distinguished by its usually terrestrial habit and thin, 3-parted leaf blades with conspicuously impressed veins. No other Costa Rican *Anthurium* has completely 3-parted blades and *A. trisectum* is not closely related to *A. subsignatum,* the only other species tending to have 3-lobed blades.

COSTA RICA. HEREDIA: La Selva (field Station of Organization for Tropical Studies) (previously Finca La Selva), *Folsom et al. 8825, 9171; Grayum 1833; Hammel 8274, 10457, 11496; MacDougall 999; Damon Smith 133; Sperry 834, 1083; Todzia 1171; Wilbur 28111, 30024, 30363, 33542* (DUKE).

Anthurium umbrosum Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1: 21. 1849. TYPE: Mexico. Oaxaca: near Mirador, *Liebmann 15790* (C, holotype; F, US, isotypes).

Anthurium liebmannii Schott, Bonplandia 7: 165. 1859. TYPE: Mexico. Oaxaca: near Teotalcingo, 5,000′, *Liebmann* (C).

Terrestrial to 1 m tall; stems 2.5–3 cm diam.; internodes very short; leaf scars to 2 cm wide; roots few, moderately thin, descending; cataphylls coriaceous, sometimes tinged with purple, 5–9 cm long, emarginate and long-apiculate at apex, drying dark tan (B & K Yellow 6/7.5), weathering into longitudinal fibers and persisting. LEAVES with petioles arching, subterete, sometimes narrowly and bluntly sulcate, or weakly flattened adaxially, 12–46 cm long; geniculum 0.7–1.1 cm long; blades medium thick, narrowly ovate to ovate-triangular, gradually long-acuminate at apex, deeply lobed at base, 20–43 cm long, 12–27 cm wide, broadest at base or midway between base and point of petiole attachment, the margin broadly undulate; anterior lobe 15–32 cm long, margin broadly convex, posterior lobes 4–14.5 cm long; sinus hippocrepiform to spathulate or parabolic, rounded to acute at apex; both surfaces semiglossy; the midrib convexly raised above, raised and conspicuously more acute below; basal veins 4–6 pairs, prominulous above, and below, third to sixth coalesced 2–3.5 cm, posterior rib straight to weakly curved, almost completely naked, the outer margin turned conspicuously upward; primary lateral veins 3–5 per side, departing midrib at ca. 50° angle, straight to weakly arching to collective vein, sunken above, flat to prominulous below; lesser veins visible, ± flat above and below; collective vein arising from the first basal vein, sunken above, raised below, 8–12 mm from the margin. INFLORESCENCE usually longer than leaves, spreading to pendent; peduncle 25–84 cm long, 2.5–3.5 mm diam., terete, at least twice as long as petioles; spathe coriaceous, green, sometimes tinged with violet-purple, oblong-lanceolate to narrowly ovate-triangular, 5.5–13 cm long, 1.5–3.3 cm wide, gradually long-acuminate at apex, narrowly inrolled to 2.5 cm long, rounded to subcordate at base, inserted at 45°–60° angle on peduncle; spadix green turning dark violet-purple to brownish at anthesis, 4.8–12.2 cm long, 5–12 mm diam. at base, 3–6 mm diam. at apex; flowers rhombic to sub-4-lobed, 3.3–4.1 mm in both directions, the sides straight to gradually to jaggedly sigmoid; 6–7 flowers visible in the principal spiral, 6–8 flowers visible in the alternate spiral; tepals matte, weakly punctate, minutely papillate with scattered droplets, lateral tepals 2–2.5 mm wide, the inner margins broadly convex; pistils green, weakly exserted just before anthesis; stigma elliptic, conspicuously raised, large stigma drop apparent shortly before stamens emerge; stamens emerging from base in a regular pattern.

FIGURES 208–211. 208. *Anthurium trisectum* Sodiro, *Croat 27362*.—209–210. *Anthurium umbrosum* Liebm., *Croat 39787*.—211. *Anthurium upalaense* Croat & Baker, *Croat 36342* (Type).

the laterals first, soon followed by alternates, complete in basal one quarter before the laterals emerge just above midway; anthers cream, held in noncontiguous circle around pistil, ca. 1 mm long, 1–1.1 mm wide; thecae ovoid, slightly divaricate; pollen cream. INFRUCTESCENCE spreading to pendent; the spathe persistent; spadix 11–13 cm long, 1.7–2 cm diam., berries usually developing in basal one half to two thirds; berries bright orange, ± globose, usually with 4 radial ridges, the apex broadly rounded to nearly truncate; mesocarp juicy, somewhat pulpy, orange with numerous raphide cells; seeds 2, obovoid, 6–7.5 mm long, 4.5–6 mm wide, 3–4 mm thick, depressed at apex. Figs. 209 and 210.

Anthurium umbrosum is endemic to Mexico and known only from northern Oaxaca, principally in the Sierra de Juárez, south of Valle Nacional on the Atlantic slope at 1,200 to 1,800 m elevation. It occurs in wet cloud forests on usually steep slopes.

The species is characterized by its terrestrial habit, moderately thick, usually narrowly ovate, long-acuminate leaf blades, green, coriaceous, lanceolate spathe, which curls under along margins, spadix green in early stages, becoming violet-purple, and orange, 4-ridged berries.

Anthurium umbrosum is in section *Belolonchium* and is closely related to *A. lancetillense.* It is distinguished from that species in having shorter, more flexible peduncles, longer, more pendent inflorescences, somewhat smaller, distinctively 4-ridged berries, and a thicker spathe. *Anthurium umbrosum* occurs at much higher elevations, *A. lancetillense* having been collected only in the Lancetilla Valley in Honduras at elevations of 10 to 600 m.

The species is also similar to *A. ovandense* from southern Oaxaca and Chiapas, but that species has a much thinner blade that is minutely undulate along the margin and that usually has anterior lobes concave along the margin.

Anthurium umbrosum is also similar to *A. lezamae* from northern Oaxaca, but that species differs in having a minutely alveolate epidermal pattern (at least on drying).

MEXICO. OAXACA: Mirador, *Liebmann 15790* (C, F, P, US); Río Mono Blanco, *MacDougall 7940* (MEXU); Teotalcingo, *Liebmann 22349* (Neg. #3903, Schott Aroid Drawing MO); along Highway 175 between Tuxtepec & Oaxaca, S of village of La Esperanza, *Croat 39787, 43905, 48026* (MO); S of Valle Nacional on road to Ixtlán de Juárez, *King 2130* (MICH); from bridge at Valle Nacional along highway to Oaxaca, *Moore & Bunting 8896* (MEXU); S of Valle Nacional, *Rzedowski 33844* (ENCB, MEXU, MO). VERACRUZ: Plan de Cediño, Munc. Acajeta, *Ventura 4665* (MICH).

Anthurium upalaense Croat & Baker, Brenesia 16 (Supl. 1): 97. 1979. TYPE: Costa Rica. Alajuela: along road between Cañas (Guanacaste) and Upala, near Río Zapote, 1.8–2.7 km south of Río Canalete, ca. 100 m elev., disturbed margin of primary forest, 25 June 1976, *Croat 36342* (MO-2381219, holotype; CR, F, isotypes; Live at MO).

Rosulate, epiphyte; stems less than 20 cm long, 1.5–2 cm diam.; leaf scars hidden by persisting cataphylls and roots; roots moderately thick and long, 2–4 mm diam., brown, moderately dense and numerous; cataphylls coriaceous, 11–22 cm long, narrowly acuminate at apex, sometimes tinged lightly with red, turning brown on drying, remaining firm and intact, ultimately deciduous. LEAVES erect-spreading; petioles (6)10–39 cm long, 7–10 mm diam., subquadrangular, broadly and sharply sulcate, prominently 3-ribbed abaxially, the sides flat to somewhat concave; geniculum 1–1.5 cm long, sometimes reddish abaxially; blades narrowly oblong-elliptic to oblong-oblanceolate, moderately thick, gradually acuminate at apex (the acumen apiculate, downturned), broadly to narrowly acute at base, (30)40–106 cm long, (4.5)8–23 cm wide, broadest at the middle or slightly above; both surfaces semiglossy; the midrib flat at base above, narrowed and becoming triangular toward apex, prominently raised below, 3-ribbed near base; primary lateral veins more than 20 per side, departing midrib at ca. 60° angle, raised above and below, ± straight to collective vein, loop-connecting in upper half; the interprimary veins flat or slightly raised above, flat and slightly darker than surface below; lesser veins less conspicuous; collective vein arising in the upper half, flat above and below, 3–5 mm from margin. INFLORESCENCE erect to spreading or arching-pendent; peduncle (18)40–48 cm long, 4–9 mm diam., terete or 1-ribbed below opening of spathe (faintly many ribbed), sometimes tinged purplish at base, longer than petioles; spathe moderately thick, yellow-green (B & K Yellow-green 6/7.5, 7/2.5, 7/5), sometimes heavily tinged with violet-purple, oblong-lanceolate to lanceolate, (4.5)8–20 cm long, 1–4 cm wide, broadest at base, gradually short-acuminate at apex, acute at base, inserted at 60°–75° angle on peduncle; spadix sessile, green to purplish (B & K Yellow-green 6/5), sometimes red, 9–30 cm long, 6–15 mm

diam. at base, 4–6 mm diam. at apex; the flowers square to rhombic, 2.3–3.4 mm long, 1.7–2.8 mm wide, the sides straight to weakly sigmoid; 7–15 flowers visible in the principal spiral, 10–20 flowers visible in the alternate spiral; tepals matte, inconspicuously pale punctate, with droplets usually after 2 or more stamens emerge, lateral tepals 0.8–1.8 mm wide, the inner margin straight to slightly convex; the pistil raised ca. 0.5 mm, green to purplish; stigma elliptic, 0.4–1.1 mm long, green, brushlike, exserted ca. 0.1 mm, with droplets for 5–15 days beginning 12–22 days before the first stamens emerge, dry and black when stamens emerge; stamens emerging rapidly from the base or near the base, emerging one at a time ca. 1 cm ahead of one another on spadix, the apical stamens usually preceding the basal ones, exserted on short greenish filaments, ca. 0.2 mm long, 0.5–1 mm wide, which retract to hold anthers in a tight circle around pistil or separately at sides of pistil; anthers pale orange, 0.5–0.6 mm long, 0.7–1 mm wide; thecae ellipsoid, scarcely divaricate, opening flat; pollen orange, fading to pale orange or lavender, white or tan. INFRUCTESCENCE pendent; the spathe reflexed; the spadix to 55 cm long, 6 cm diam.; berries oblong, red, tapered to both ends, 9–15 mm long, acute at apex, emerging ± uniformly throughout spadix, well above tepals before fully mature; mesocarp mealy, sweet, white; seeds 2, oblong, to 4 mm long, 3 mm wide, 2.5 mm thick, creamy white, obliquely truncate at apex with a short appendage, greenish at base. Figs. 211 and 212.

The species is known from the Atlantic slope of Nicaragua and Costa Rica at elevations from near sea level to usually less than 600 m in regions of tropical wet forest, premontane wet forest, and wetter parts of tropical moist forest life zones. A collection from Cartago Province, northeast of Río Grande de Orosi at 1,300 m is apparently also this species.

Anthurium upalaense is a member of section *Pachyneurium* and is apparently most closely related to *A. concolor* K. Krause from Panama but differs in having the inflorescence pendent, the spadix long-tapered and more or less green at anthesis, the spathe longer and recurled, the fresh anthers pale orange, the major lateral veins scarcely raised, often forming a collective vein from near the middle or above, the reticulate veins clearly visible when fresh, weakly raised and prominulous when dried. *Anthurium concolor,* on the other hand, has the inflorescence stiffly erect, the spathe usually less than 10 cm long, usually not recurled at apex, the spadix not tapered, dark purple-violet, and usually less than 7 cm long at anthesis. Its flowers form minute globules of nectar on the tepals and the pollen is pale violet-purple, its major lateral veins are prominently raised and seldom form a collective vein except near the apex, and the reticulate veins are more or less obscure. *Anthurium concolor* is known only from the Atlantic slope in central Panama.

COSTA RICA. Cultivated at Kew, from Costa Rica, *N. E. Brown s.n.* (K); *Bull 467/1873* (K). ALAJUELA: W of Fortuna, NW of New Volcán Arenal, *Taylor & Taylor 1170* (NY); San Juan de Lajas, *Austin Smith 1498* (NY); near Artezalea and Methodist Rural Center, NE of Ciudad Quesada, *Molina et al. 17264* (EAP, F); vicinity Los Chiles, Río Frío, *Holm & Iltis 771* (NY); *811* (P, U); road between Cañas and Upala, N of Río Zapote, *Croat 36342* (CR, F, MO); *36380* (MO); road between Cañas and Upala, NNE of Bijagua, *Croat 36319* (MO); S of Canalete near the Río Zapote, and along the new road to Upala, *Burger & Baker 1001* (CR, F, MO, US); *9964* (F); NNE of Bijagua along the new road to Upala, *Burger & Baker 9859* (CR, F); Lake Arenal, Alto de la Carpintera, near Tilarán, *Brenes 18194, 18195* (CR). CARTAGO: NE of Río Grande de Orosi at Tapantí, *Utley 5062* (MO); Forest of Tuis, near Turrialba, *Pittier 12720* (US); Lake Bonilla, *Pacheco 92* (F). GUANACASTE: El Arenal, *Standley & Valerio 45328* (US). HEREDIA: Finca La Selva, Puerto Viejo de Sarapiquí, *Croat 44297* (MO); near Puerto Viejo along road to Río Sucio, *Croat 35708* (MO); SW of Puerto Viejo along road to San José, *Burger & Matta 4343* (F, CR). LIMÓN: between Hone Creek and NW on a trail paralleling the Río Carbón, *Utley & Utley 660* (F); Taskí, Talamanca Valley, *Tonduz 9507* (BR, CR); *Pittier 9509* (BR); Forests of Shirores, Talamanca, *Tonduz 9228* (BR); Hamburg Finca on Río Reventazon below Cairo, *Standley & Valerio 48869* (US); along Hwy. 32 near Río Madre, SW of Limón, *Croat 43305* (MO); vicinity of Bribrí near Río Catarata, *Croat 43221* (MO); general Vicinity Limón, *Burger & Burger 8446* (CR, F); along shore at Cahuita, *Baker & Burger 17A* (CR, F); *17B* (CR, F, MO); along the new road between Limón and Puerto Viejo, *Baker & Burger 174* (F). SAN JOSÉ: Forests of Las Vueltas, Tucurrique, *Tonduz 13319* (US).

NICARAGUA. MATAGALPA: Cerro Musún, W & NW side above Salto Grande of Quebrada Negra and in valley of Río Bilampí, *Neill 1782* (MO). RÍO SAN JUAN: *Neill 1552* (MO). ZELAYA: along stream N of settlement "Las Mercedes," *Vincelli 328A* (MO).

Anthurium utleyi Croat & Baker, Brenesia 16 (Supl. 1): 100. 1979. TYPE: Costa Rica. Alajuela: 2 km N of Ángeles Norte de San Ramón, 4,000′, *Luteyn 3695* (DUKE-233270, holotype).

Epiphyte; stems short, densely covered by

FIGURES 212–215. 212. *Anthurium upalaense* Croat & Baker, *Croat 43305*.—213–214. *Anthurium validifolium* K. Krause, *Croat 10667*.—215. *Anthurium verapazense* Engl., *Boutin 5122*.

cataphyll fibers; roots few, moderately long, descending, 2–3 mm diam.; cataphylls 3–6 cm long, apiculate at apex, drying tan, weathering into dense, tangled, persisting fibers. LEAVES spreading; petioles 8.5–24 cm long, 2–5 mm diam., subterete, shallowly sulcate to weakly flattened adaxially, rounded abaxially; geniculum 0.8–2 cm long; blades moderately thick, oblong to oblong-elliptic or oblong-oblanceolate, acuminate at apex, acute to obtuse or narrowly rounded at base, 15–35 cm long, 3.3–7.5 cm wide, broadest near middle or just above; both surfaces punctate, conspicuously black punctate on lower surface; midrib convexly raised near base above, narrowed toward apex, prominulous below; primary lateral veins 14–20 per side, departing midrib at ca. 45° angle, ± obscure above, scarcely visible below; collective vein arising from the base, scarcely visible above and below, 2–7 mm from margin (often more remote from margin in lower half of blade than in upper half). INFLORESCENCE usually erect-spreading, equalling or shorter than leaves; peduncle 10–27 cm long, 2–3 mm diam., as long as or longer than petioles; spathe green to purple, narrowly lanceolate, 3.4–6 cm long, 1–1.5 cm wide, broadest at base, acuminate at apex, obtuse to rounded at base, inserted at 45° angle on peduncle; stipe 1–6 mm in front, to 3 mm in back, ca. 2 mm diam.; spadix green to brownish-red or purplish-green, 2–15 cm long, 7–9 cm diam. at base, 3–5 mm diam. at apex; flowers rhombic to 4-lobed, 2.1–2.5 mm long, 2–2.5 mm wide, the sides sigmoid; 4–5 flowers visible in the principal spiral, 5–9 flowers visible in the alternate spiral; tepals glossy, densely, weakly and minutely papillate, lateral tepals 1.2–2.5 mm wide, the inner margin convex; pistils emergent 0.3–0.5 mm, white; stigmas elliptic, ca. 0.4 mm long with small droplets before stamens emerge; stamens emerging rapidly from the base, lateral stamens preceding alternates by only 1–2 spirals, exserted on filament ca. 0.5 mm long, which quickly retract to hold anthers at edge of tepals; anthers ca. 0.4 mm long, 0.6 mm wide; thecae white, dish-like, ellipsoid; pollen white. INFRUCTESCENCE with orange, ovoid berries. Fig. 216.

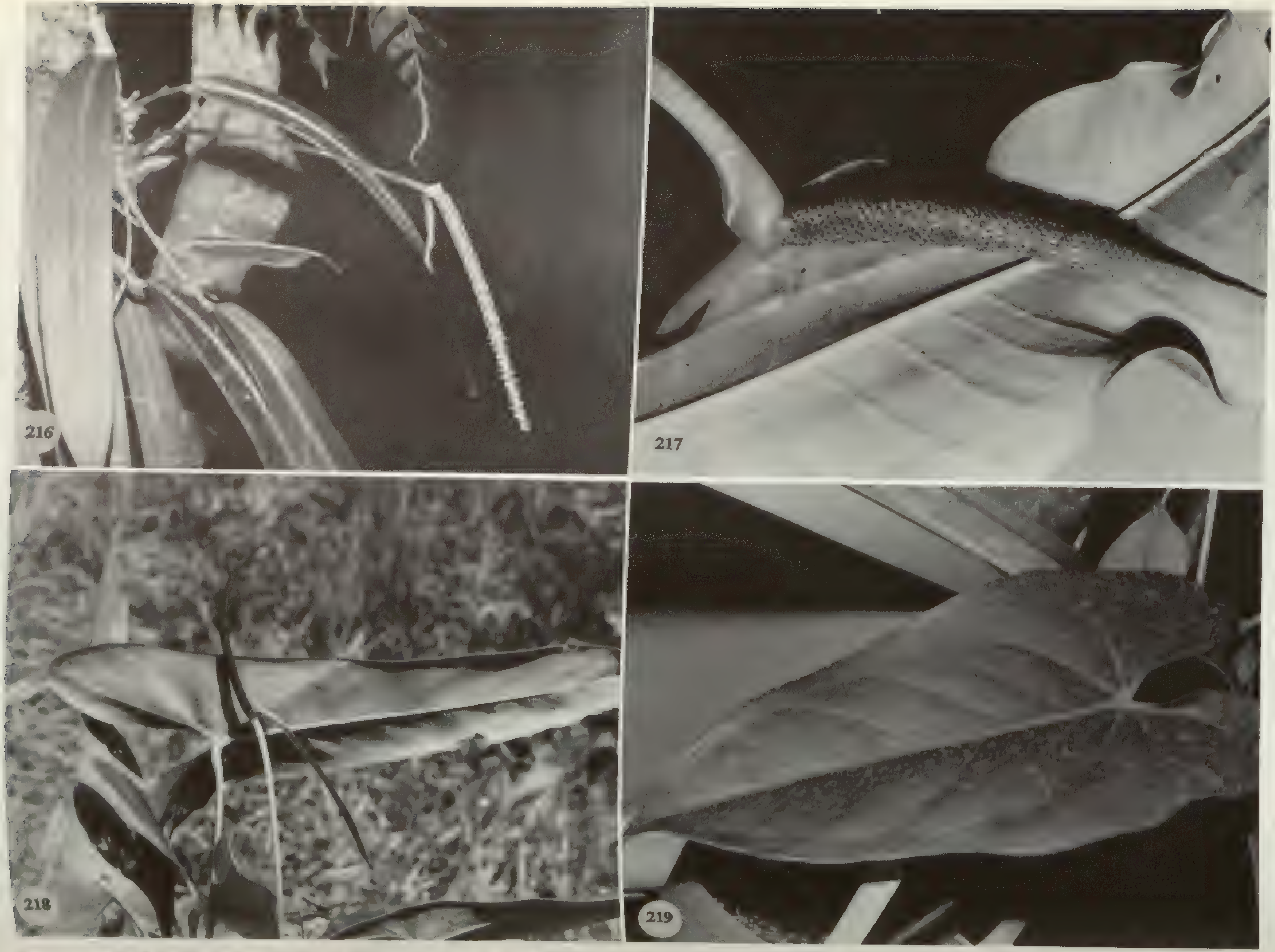
The species is known from Costa Rica in forests in vicinity of San Ramón and near Monteverde at elevations of 760 to 1,690 m.

Anthurium utleyi is in section *Porphyrochitonium* and is most closely related to *A. friedrichsthalii*, but differs from it in its shorter and broader leaves and its beaked berries. The species is named in honor of John and Kathy Utley, who made many important collections of Araceae in Costa Rica.

COSTA RICA. ALAJUELA: S of Balsa de San Ramón, *Lent 3519, 3520* (F); *Utley & Utley 1851* (F); Los Ángeles de San Ramón, *Brenes 14844a* (NY); N of Ángeles Norte de San Ramón, *Luteyn 3695* (DUKE); Catarates de San Ramón, *Brenes 14222* (NY); along road out of San Ramón, beyond Ángeles Norte, *Luteyn et al. 4274* (DUKE). GUANACASTE: near E edge of Monteverde Preserve along road between Santa Elena and Monteverde, ca. 2.5 miles from Santa Elena, *Croat 47135* (MO). HEREDIA: S of Cariblanco, *Croat 35795* (MO). ALAJUELA & PUNTARENAS: Monteverde, *Palmer 90* (NY); *Dryer 1337* (F); *Luteyn 3398* (DUKE); upper drainage of Río Peñas Blancas below Monteverde Cloud Forest, *Lawton 1165* (F).

Anthurium validifolium K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11: 607. 1932. TYPE: Panama. Chiriquí: forests along Río Ladrillo, above El Boquete, 1,200–1,300 m, *Pittier 3052* (US).

Epiphyte; stems to 16 cm long, 12 cm diam.; leaf scars 2.5 cm wide; roots numerous, green, descending, 1–1.5 cm diam.; cataphylls subcoriaceous, ca. 20 cm long, acuminate at apex, drying tan (B & K Yellow-red 9/10), persisting ± intact. LEAVES erect-spreading; petioles 20–27 cm long, 7–10 mm wide, ± quadrangular, broadly and shallowly sulcate; geniculum 3–3.5 cm long; blades lanceolate, coriaceous, 47–69 cm long, 10–19 cm wide, acuminate at apex, rounded at base, broadest at middle, the margins broadly undulate; both surfaces matte; midrib broadly and convexly raised at base above, more acutely raised toward apex, diminishing and sunken at apex, raised and square at base below, more acute toward apex; primary lateral veins numerous, departing midrib at 60°–70° angle, ± straight, arching near margin, sunken in valleys above, raised below; interprimary veins scarcely visible; collective vein arising from one of the primary lateral veins in the apical one quarter of the blade, 5–6 mm from margin, weakly sunken above, raised below. INFLORESCENCE spreading, shorter than leaves; peduncle 33–39 cm long, 9–12 cm diam., subterete, twice as long as petioles; spathe coriaceous, dark green (B & K Yellow-green 5/10), turning yellow, ovate-lanceolate, 16–17 cm long, ca. 4 cm wide, acuminate at apex, rounded at base, inserted at ca. 45° angle



FIGURES 216–219. 216. *Anthurium utleyi* Croat & Baker, *Croat 47135.*—217. *Anthurium validifolium* K. Krause, *Croat 10667.*—218. *Anthurium verapazense* Engl., *Croat 41683.*—219. *Anthurium verapazense* Engl., *Croat 40628.*

on peduncle, reflexed and held parallel to peduncle; stipe 7–13 mm long in front, ca. 3 mm long in back; spadix pale lavender to violet-purple (B & K Purple 6/5 to 5/2.5), green at apex in early stages, 15–23 cm long, 1.2–3.5 cm diam. at base, 5–10 mm diam. at apex; flowers rhombic, 3–3.5 mm long, 3.1–3.6 mm wide, the sides straight to weakly sigmoid; 7–8 flowers visible in the principal spiral, 8–10 flowers visible in the alternate spiral; tepals matte, lateral tepals 1.5–1.8 mm wide, the inner margin broadly rounded; pistils scarcely emergent, green; stigma elliptic, ca. 0.6 mm long, droplets apparent for ca. 1 week before stamens emerge; stamens emerging promptly from near base (but usually not the lowermost spiral) or sometimes at middle, the lateral stamens emerging in ca. three quarters the length of spadix before alternates emerge; anthers yellow-orange, held inward and partially covering stigma at level of tepals, ca. 1 mm long, 1.2 mm wide; thecae oblong-ellipsoid, scarcely divaricate; pollen yellow-orange (B & K Yellow-red 8/5). INFRUCTESCENCE pendent; spathe twisted; spadix 24–26 cm long, 2.3–2.5 mm diam.; berries bright orange, obovoid, flattened at apex, 0.8–15 mm long, pericarp thin, ± transparent, orange; mesocarp fleshy, orange with minute raphide cells; seeds 1–2, ovoid, pale yellow, tinged brown at apex and base with somewhat flattened appendage at both ends, encased in a somewhat dry, sac-like structure. Figs. 213, 214, and 217.

Anthurium validifolium is a member of section *Pachyneurium*. It is known for certain only from Chiriquí Province of Panama, but a cultivated plant at Las Cruces Botanical Garden near San Vito de Java near the Panamanian border in Costa Rica may be a native to the area according to the owner, Mr. Bob Wilson. Most collections have been made in lower montane wet forest and lower montane rain forest from 1,600 to 2,000 m. One Panamanian collection was made in premontane wet forest, which corresponds to the life zone at the Las Cruces Botanical Garden. This further substantiates that *A. validifolium* is also native to Costa Rica.

Anthurium validifolium is characterized by its large, moderately thick, lanceolate leaf blade, lavender to purple spadix, and bright orange, obovoid berries. It is perhaps most closely related to *A. seibertii* and *A. protensum*, which share a similar inflorescence and orange berries. It differs from both of those species in having broader and thicker leaf blades. Its petiole is subquadrangular and somewhat intermediate between the terete petiole of *A. protensum* and the sharply quadrangular petiole of *A. seibertii*. Although this suggests *A. validifolium* may be a hybrid between *A. protensum* and *A. seibertii*, its thicker, proportionally shorter blades are not found on either of these species.

COSTA RICA. PUNTARENAS: Las Cruces Botanical Gardens, *Croat 44445* (MO).

Anthurium verapazense Engl., Pflanzenr. IV 23B: 191. 1905. TYPE: Guatemala. Alta Verapaz: Cubilhuitz (Finca Cubilhuitz 15°40′N, 90°25′W) elev. 350 m, *H. von. Tuerckheim 7788* (US, holotype).

Usually epiphytic, sometimes terrestrial; stems 4–8 cm long, 5–6 cm diam.; internodes and leaf scars hidden by persisting cataphylls and thick, descending, dark brown roots; cataphylls subcoriaceous, 6–9 cm long, acuminate at apex, sometimes tinged red-violet, subapical apiculum ca. 2 mm long, drying dark brown (B & K Yellow 4/7.5), persisting as reticulate fibers. LEAVES with petioles erect-spreading, 26–61 cm long, 6–7 mm diam., subterete; geniculum 3–4 cm long, conspicuously sulcate; blades moderately thick, triangular, sometimes ovate-triangular, gradually acuminate at apex, prominently lobed at base, 24–60 cm long, 14–27 cm wide, broadest at base or sometimes at point of petiole attachment; anterior lobe 24–49 cm long, convex to almost straight; posterior lobes 8–17 cm long; sinus hippocrepiform to spathulate to sometimes ovate, usually rounded at apex; both surfaces semiglossy, the lower surface densely punctate; midrib acutely raised above, diminished and sunken from just above the middle to the apex, convexly raised below; basal veins 4–6 pairs, the first free to base, those remaining coalesced 2.5–4 cm, sunken above, raised below; primary lateral veins 7–9 per side, departing midrib at 45°–55° angle, loop-connecting to collective vein, sunken above, prominulous below; lesser veins less conspicuous; collective vein arising from the first basal vein, sunken above, raised below, 4–6 mm from the margin. INFLORESCENCE arching-pendent; peduncle 53–90 cm long, 4–6 mm diam.; spathe moderately thin, oblong-lanceolate, green (B & K Yellow-green 7/10), sometimes tinged violet-purple at margins, 8.5–15 cm long, 1–2 cm wide, broadest near base, narrowly acuminate at apex, obtuse at base, inserted at 45° angle on peduncle; spadix violet-purple (B & K Red-

purple 2/5), 10–25 cm long, 6.5–8 mm diam. at base, 3–5 mm diam. at apex; flowers rhombic, 3.6–3.8 mm long, 2.3–2.8 mm wide, the sides straight parallel to the spiral, gradually sigmoid perpendicular to the spiral; 6–7 flowers visible in the principal spiral, 8–10 flowers visible in the alternate spiral; tepals matte to semiglossy, obscurely and sparsely punctate, minutely papillate, the lateral tepals ca. 2 mm wide, the inner margin ± concave and turned up against pistil; pistils weakly emergent, violet-purple slightly paler than tepals; stigma slit-like, oblong, ca. 0.6 mm long; stamens emerging in a moderately rapid sequence from the base, the laterals first, followed shortly by alternates, the leading stamens preceding third and fourth by several spirals, briefly exserted on purplish filaments, withdrawing to level of tepals; anthers yellow, ca. 0.2 mm long, 0.6 mm wide, held in a close, tight circle around pistil; thecae ellipsoid, divaricate; pollen lemon-yellow fading to white. INFRUCTESCENCE pendent; spadix 15–34 cm long, 1–2.8 cm diam.; spathe often withered or deciduous; berries subglobose to obovoid, rounded at apex, developing in the basal one third to one half, ca. 7 mm long, ca. 6.7 mm diam.; mesocarp juicy, with numerous whitish raphide cells; seeds 1–2, 3.5–4.2 mm long, 3–3.6 mm wide, 2–2.5 mm thick, broadly ellipsoid to subrounded, flattened, emarginate at apex, pale purplish-violet with numerous, clear punctations, the surface sticky, the hypocotyl small. Figs. 215, 218, and 219.

Anthurium verapazense ranges from Belize to Guatemala along the Atlantic slope in principally moist forest habitats at elevations of 100 to 800 m. It is easily confused with *A. lucens,* which is more wide ranging, occurring throughout much of Chiapas and northern Guatemala as well as in northern Honduras. The latter is generally found at higher elevations, from 350 to 2,000 m.

Anthurium verapazense is in section *Belolonchium* and is distinguished by its usually long, narrow spathe, much less than half as long as the spadix at anthesis. In addition the inflorescence is usually 1.5 to 3 times longer than the longest petioles. *Anthurium lucens* differs in having a relatively short spadix with the spathe usually over half as long as the spadix at anthesis, by the relatively shorter inflorescence which is shorter than the leaves or rarely more than 1.5 times longer than the petioles, and by the red, obovoid berries with 2 relatively much larger seeds.

Leaf shape in *A. verapazense* is greatly variable, ranging from deltoid to ovoid to deltoid-hastate. The lobes may be directed downward, sharply outward, or even somewhat inward. Even plants within a single population may show great variability. Neither *A. verapazense* or *A. lucens* show correlation with regard to leaf shape although collections from the same area show similar trends in variation. Worthy of mention is a collection of *A. verapazense* made by Dr. R. Tejada (*307*) purportedly collected in Mazatenango, a town on the Pacific slope. I believe it is unlikely that the species ever occurred there and perhaps there was (in 1914) another village called Mazatenango located on the Atlantic slope or perhaps the collection was cultivated in Mazatenango. Other species were also collected by Tejada at Mazatenango that are likewise not believed to have ever occurred there.

It is possible that additional work will prove that the taxon as constituted here consists of two species. A live collection made by Hans Wiehler near Purulhá in Alta Verapaz (Guatemala) and cultivated at Selby Botanical Gardens produced subglobose, red-orange berries that had 6–9 small seeds. This has been vouchered as *Madison 3739.* A second Madison collection (*6965*) from a live plant purportedly also from Purulhá had similar berries with 2 large seeds. These were similar to the berries of other collections studied, namely *Jones & Facey 3389* from the department of Izabal and *Boutin 5122* from Belize. The latter is live at the Missouri Botanical Garden. These drastic differences are not easily explained and have not been exhibited in other species of *Anthurium.* The problem warrants additional investigation.

BELIZE. BELIZE DISTRICT: S of Gales Point, cultivated at Kew, *Hunt 7043* (K, MO); Gracy Rock, Sibun River, *Gentle 1667* (MICH, MO, NY); Manatee Lagoon, *Peck 24* (GH); 22 miles south of Western Highway, *Dwyer & Liesner 1512* (MO); *Croat 23852* (MO). CAYO DISTRICT: no other location, *Lundell 6341* (MICH); La Flor hunting camp, S of Grano de Oro, *Gentry 7835* (MO); Mountain Pine Ridge, *Bartlett 13054* (MICH, US); *Hunt 416* (US); *Lundell 6780* (MICH); *Wiley 325A* (MO); between San Luis and Cuevas at Río Macal, *Croat 23533* (MO); Waterhole Camp near Vaca, *Gentle 2445* (MICH). STANN CREEK DISTRICT: Stann Creek Railroad, *Schipp S177* (F). TOLEDO DISTRICT: Maya Mountains, Union Camp, *Boutin & Schlosser 5122* (MO).

GUATEMALA. ALTA VERAPAZ: Chamá, *Johnson 896* (UCLA); along road to Finca Trece Aguas, N of Church in Senahú, *Luteyn & Almeda 3523* (DUKE); vicinity of Laguna Sapalau, SW of Sibicté, *Steyermark 44924* (MO); 4–9 miles up road to Oxec, along gravel road which turns N off Highway 7E between Tucurú and El

Estor ca. 6 km NE of Panzós, *Croat 41605, 41683* (MO); vicinity Purulhá, cultivated at Selby, *Madison 3739, 6965* (MO). IZABAL: vicinity Exmibal, NW of Lake Izabal, *Jones & Facey 3389* (LL, NY). PETÉN: Poptún, *Molina 15613* (NY).

MEXICO. CHIAPAS: Finca Prusia, Mapastepec, NW of Huixtla, *MacDougall 337* (CAS, DS, MEXU); Lagos de Montebello, 3 mi W of Dos Lagunas, *Croat 46656* (MO); Ocozocoautla de Espinosa, *Breedlove 27489* (DS); N of Ocozocoautla de Espinosa on gravel road to Apitpac, *Croat 40628* (MO). VERACRUZ: Lake Catemaco, Soteapan, *Beaman 6142* (XAL).

Anthurium watermaliense Hort. ex L. H. Bailey, Stand. Cycl. Hort. 1: 303. 1922. TYPE: Colombia. Not seen (introduced into horticulture via Watermall, Belgium).

Terrestrial; stems to 25 cm long; cataphylls thin, 4.5–9 cm long, rounded at apex, weathering into coarse fibers. LEAVES with petioles erect-spreading, 12–88 cm long, ± terete, weakly flattened or sulcate; geniculum 1–1.5 cm long; blades ovate-triangular, moderately thick, gradually acuminate at apex, deeply lobed at base, 30–60 cm long, 19–36 cm wide; the anterior lobe 20–45 cm long; posterior lobes 14–26 cm long; sinus parabolic to hippocrepiform; both surfaces semiglossy; midrib convexly raised above and below; basal veins 5–8, the second to eighth coalesced 4.5–8 cm, prominulous above and below, yellow below, posterior rib mostly naked, weakly turned up; primary lateral veins 4–8 per side, departing midrib at 40°–45° angle, prominulous in valleys above, prominulous below; lesser veins less conspicuous; collective vein arising from the first or second basal vein, raised above and below, 3–6 mm from margin. INFLORESCENCE spreading, shorter than leaves; peduncle 12–66 cm long, 5–7 mm diam., spathe lanceolate-triangular, green to dark violet-purple, subcoriaceous, 5–21 cm long, 2.3–8.5 cm wide, long-acuminate at apex, obtuse to rounded at base, inserted at 75° angle on peduncle; stipe 0.3–3 cm long; spadix white to greenish, yellow or purple, 7–10 cm long, 5–10 mm diam. at base, 2–5 mm diam. at apex; the flowers rhombic to 4-lobed, 1.5–3.4 cm long, 1.8–3.1 mm wide, the sides straight to jaggedly sigmoid; 5–12 flowers visible in the principal spiral, 6–16 flowers visible in the alternate spiral; tepals matte, green with purple on inner and outer edges, punctate, with sparse droplets when stamens are fresh, lateral tepals 1.5–2.2 mm wide, the inner margin convex to ± straight; pistil dark green, glossy, raised, weakly exserted just before stamens emerge; stigma narrowly elliptic, ca. 0.5 mm long, with papillae not exserted, a small stigma droplet apparent 2–3 days before stamens emerge, dry and gray as stamens open; stamens emerging rapidly from base, or sometimes scattered throughout, exserted on short translucent filaments, 0.3–0.4 mm long, 0.6 mm wide, which retract holding stamens in a tight cluster over pistil; anthers creamy white, 0.9 mm long, 0.9–1 mm wide; thecae ellipsoid, divaricate; pollen white. INFRUCTESCENCE with spadix to 22 cm long; berries yellow to orange, ovoid to obovoid, beaked, 1–1.5 cm long. Figs. 224 and 225.

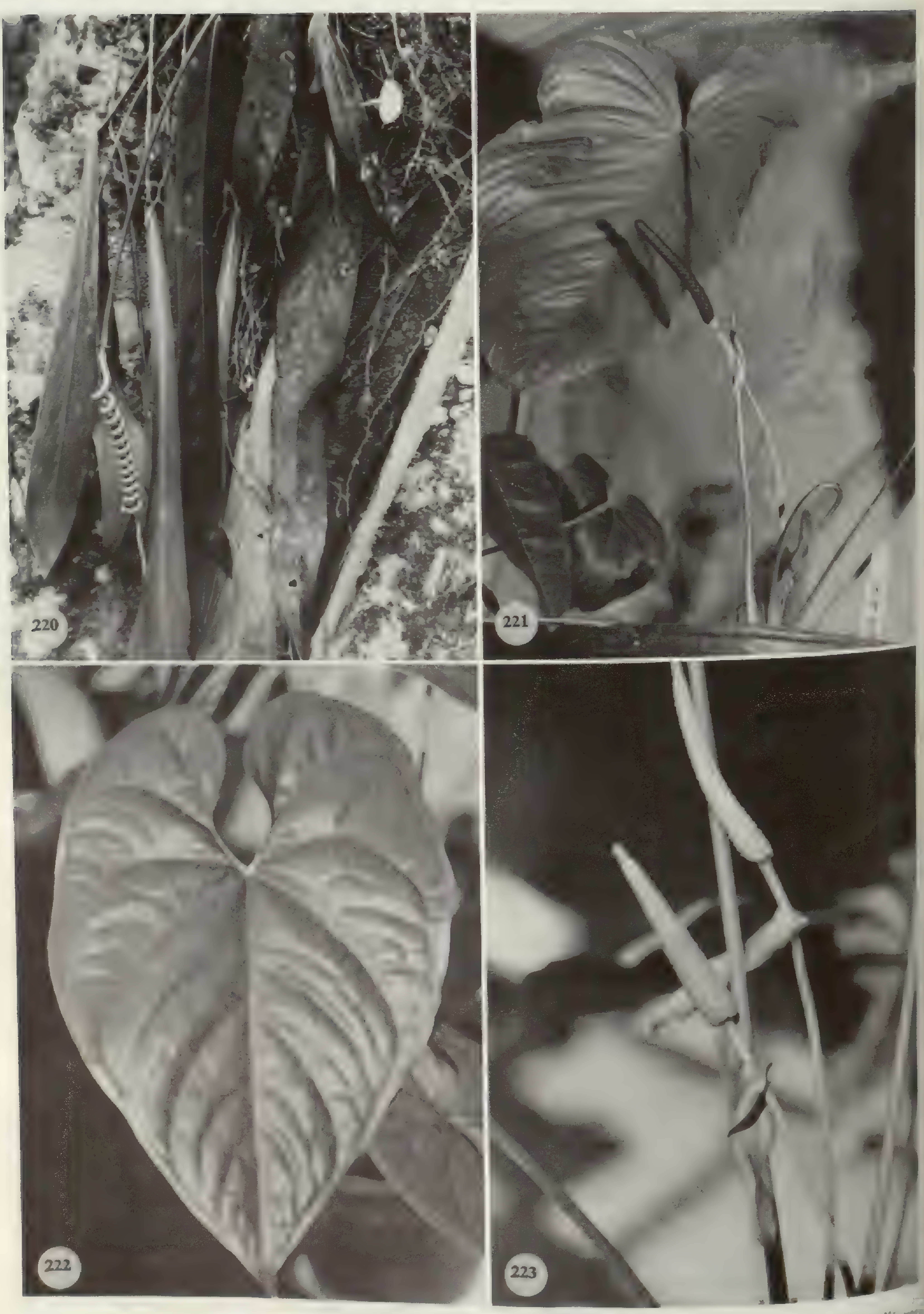
The species is known from Costa Rica to Colombia, usually from 750 to 2,400 m elevation in premontane rain and lower montane rain forest. Some populations also occur near sea level in tropical moist forest and premontane wet forest. The species is extremely variable, especially in leaf size and shape, and spathe and spadix color. It is strange that the species has not been found in tropical wet forest or at elevations between 100 and 700 m. Perhaps further study will show that the lower elevation populations are a distinct species.

Anthurium watermaliense is an atypical member of section *Pachyneurium* and is not generally confused with any other species in Central America. It can be recognized by the ovate-triangular to sub-3-lobed leaf blades, the broad, frequently dark purple spathe, green to purple, stipitate spadix with long-exserted stamens, and yellow to orange berries.

The species has long been known in horticultural circles, being first introduced from Colombia to Watermall, Belgium, by an unknown collector; although the name was validated by a short note by Bailey in the Standard Cyclopedia of Horticulture (1: 303. 1922), no type was designated. I have as yet seen no Colombian material of the species and therefore decline to name a lectotype at this time.

COSTA RICA. No other location, *Lankester 349-49* (K). ALAJUELA: Monteverde Biological Reserve, *Kennedy & Guidon 3799* (MO). CARTAGO: Camino Raiz de Hule, SE of Platanillo, *Croat 36713* (MO); vicinity Palo Verde, *Luteyn & Wilbur 4376* (MO). HEREDIA & SAN JOSÉ: S facing slopes of Cerro Zurquí, *Almeda 3706* (MO); Río Para Blanca, Cerro de Zurquí, *Burger et al. 9342* (MO); Cerro Zurquí, N of San Luis Norte, *Stolze 1548* (MO). LIMÓN: between Bribrí and Bratsi, along Río Sixaola, *Burger et al.* 10444 (MO); vicinity Bribrí, Río Catarata, *Croat 43224* (MO); N of Limón, *Lent 347* (MO).

Anthurium wendlingeri G. M. Barroso, Bol. Soc. Venez. Ci. Nat. 26: 151. 1965. TYPE: Costa



Figures 220–223. 220. *Anthurium wendlingeri* G. M. Barroso, *Croat 34295*. — 221. *Anthurium williamsii* K. Krause, *Croat 36628*. — 222–223. *Anthurium yetlense* Matuda, *Croat 39768*.

FIGURES 224–227. 224–225. *Anthurium watermaliense* Hort. ex L. H. Bailey, *Croat 38129*.—226–227. *Anthurium wendlingeri* G. M. Barroso, *Croat 37329*.

Rica. Cartago: Turones (Pavones), Turrialba, 700 m, *Wendlinger s.n.* (RB, holotype).

Pendent epiphyte; stems ca. 20 cm long; the internodes 1.5–2 cm long, except near apex; roots moderately thick; cataphylls moderately thick, 5.5–15 cm long, acuminate at apex, drying brown, weathering into coarse persistent, longitudinal fibers. LEAVES spreading-pendent; petioles terete, (5)8–30 cm long, 2–4 mm diam.; geniculum 1–1.5 cm long; blades oblong, moderately thick, 32–80 cm long, 3–11 cm wide, acuminate at a apex, round to truncate at base; upper surface weakly velvety, obscurely and sparsely glandular-punctate, lower surface semiglossy, sparsely glandular-punctate; midrib convexly raised at base above, more acute toward apex, diminishing and flat at apex, raised at base below, flat from ca. midway to apex; primary lateral veins 11–24 per side, departing midrib at 30°–40° angle, raised and nearly obscure above, flat below; lesser veins obscure; collective vein arising from the lowermost primary lateral vein, weakly sunken above, flat to weakly raised below, 5–9 mm from margin. INFLORESCENCE spreading to pendent, usually shorter than leaves; peduncle 13–42 cm long, 3–7 mm diam.; spathe moderately thin, pale green tinged purplish, ± oblong, 7–11 cm long, 8–13 mm wide, gradually acuminate at apex, inserted at ca. 45° angle on peduncle, withering and curling horizontally or deciduous; spadix pale green to white or grayish-white, straight when young, becoming spiralled in age, 12–80 cm long, 3–5 mm diam. at base, narrowly-tapered to apex; flowers ± 4-lobed, 3–3.1 mm long, 2.4–2.6 mm wide, the sides smoothly sigmoid; 4–5 flowers visible in the principal spiral, ca. 10 flowers visible in the alternate spiral; tepals matte, weakly punctate, minutely papillate, the lateral tepals 1.6–1.7 mm wide, the inner margin broadly rounded; pistils weakly emergent, pale green, glossy; stigmas linear, 0.3 mm long; lateral stamens emerging scattered throughout length of spadix, alternate stamens soon following with no apparent pattern; anthers cream, held at edge of tepals against sides of pistil, ca. 0.7 mm long, ca. 0.6 mm wide; thecae ellipsoid, not divaricate; pollen creamy-white. INFRUCTESCENCE pendent; berries reddish, ± oblong or globose, ca. 5 mm long, flattened at apex with a central depression. Figs. 220, 226, and 227.

Panamanian plants considered *A. wendlingeri* range from Veraguas in the west to Coclé, Panamá, and Colón Provinces on the Atlantic slope and along the Continental Divide in tropical wet forest and premontane rain forest at elevations of 350 to 900 m.

Anthurium wendlingeri was described from live material collected in Cartago Province of Costa Rica. The type description reports the inflorescences as being "atropurpureus" and no other flowering material has been seen for Costa Rica. Panamanian collections closely matching this species in vegetative condition, habit and all other aspects consistently have spadices that are white to grayish-white at anthesis. More material must be seen from Costa Rica to determine if those populations really do have purple spadices and to determine if the Panamanian plants are the same or if they should be considered distinct. One collection from Coclé (*Croat 37329*) was reported to have a reddish spadix but it has consistently flowered with a white spadix in cultivation.

The species is in section *Porphyrochitonium* and is distinguished by its coriaceous, oblong, glandular-punctate leaf blades, very elongate, whitish, corkscrew-like spadix and reddish berries. The blades are weakly velvety and obscurely punctate above and below. It is most easily confused with another Panamanian species, *A. pendens* Croat (ined.), which occurs in similar habitats in Colón and Panamá Provinces. That species differs, however, in having narrowly oblanceolate blades that are acute at the base and that dry conspicuously blackened, and especially by its stouter, relatively short, greenish-purple to brownish spadix, which never coils.

COSTA RICA. HEREDIA: S of Cariblanco, *Croat 35830* (MO).

Anthurium williamsii K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11: 610. 1932. TYPE: Panama. Darién: near Cana, *Williams 817* (not seen).

Terrestrial; stems short; cataphylls subcoriaceous, 3–12 cm long, acute at apex, drying brown (B & K Yellow-red 2/5), weathering into longitudinal fibers. LEAVES with petioles erect-spreading, 23–61 cm long, 5–8 mm diam., subterete, sometimes faintly 2–3- or more ribbed; geniculum 2–3.5 cm long; blades narrowly ovate to broadly ovate, thin, ± membranous, long acuminate to cuspidate at apex, lobed at base, 26–48 cm long, 19.5–36 cm wide, broadest at middle; anterior lobe 21–35 cm long, the margins

broadly rounded; posterior lobes 9–16 cm long from apex of sinus to outermost point; sinus triangular, sometimes closed, acute at apex; matte to semiglossy on both surfaces; midrib weakly and convexly raised above, prominently raised below; basal veins 6–7 pairs, usually all free to base; posterior ribs absent; primary lateral veins 8–10 per side, departing midrib at 35°–50° angle, sunken in valleys above, prominently raised below, basal and primary lateral veins drying conspicuously yellow; lesser veins scarcely visible; collective vein arising from one of the uppermost basal veins, 2–3 mm from the margin. INFLORESCENCE erect; peduncle (16)40–53 cm long, 4–5 mm diam., shorter or equalling petiole; spathe membranous, pale green (B & K Green 7/5), sometimes withering early, lanceolate, 7–12.5 cm long, 1.5–2.8 cm wide, caudate-acuminate at apex, subcordate at base, inserted on peduncle at 25° angle; stipe 3–5 mm long in front, 1–3 mm long in back; spadix violet-purple or green tinged violet-purple, (7)11–20 cm long, (6)7–10 mm diam. at base, 4–5 mm diam. at apex; flowers square, 2.5–3 mm long, 2.1–3 mm wide, the sides weakly sigmoid; 4–5 flowers visible in the principal spiral, 7–9 flowers visible in the alternate spiral; tepals glossy, lateral tepals 1.7–2 mm wide, the inner margin convex; pistils dark purple, scarcely emergent before anthers emerge; stigmas minute, scarcely visible; stamens emerging rapidly from the base, the leading stamens emerging at apex as third and fourth are emerged two-thirds the length of spadix, exserted on white, translucent, flattened filaments, ca. 0.4 mm long, retracting to hold anthers over pistil; anthers purple to red-violet 0.4–0.5 mm in both directions; thecae ellipsoid; pollen orange (B & K Yellow-red 7/5). INFRUCTESCENCE pendent; berries deep red-violet, obovoid; mesocarp gelatinous with numerous raphide cells; seeds 2, pale yellow, tinged reddish brown at apex, green at base, ovoid, flattened, 4.6 mm long, 3.3–3.7 mm wide, 2 mm thick, encased in a sticky substance. Fig. 221.

Anthurium williamsii ranges from Costa Rica to Ecuador from near sea level to 1,800 m elevation. In Costa Rica it has been collected in premontane rain forest. In Panama it has been collected in premontane wet forest, tropical wet forest, and premontane rain forest.

The species is placed in section *Polyneurium* and is closest to *A. cuspidatum* (see that species for differences). One collection from Costa Rica (*Croat 36721*) is somewhat intermediate between *A. williamsii* and *A. cuspidatum* and may be a hybrid.

COSTA RICA. CARTAGO: vicinity of Moravia, *Croat 36628, 36721, 36790* (MO).

Anthurium yetlense Matuda, Anales Inst. Biol. Univ. Nac. México 32: 151, Fig. 7. 1961. TYPE: Mexico. Oaxaca: near Yetla (San Mateo Yetla?), January 14, 1959, *MacDougall 410* (MEXU, holotype).

Terrestrial; stems ca. 30 cm long, 3.5 cm diam., green; internodes short; roots thick, tan, pubescent, directed downward; cataphylls subcoriaceous, 7–9 cm long, tinged red-violet, rounded at apex, acumen apiculate, subapical apiculum 2–5 mm long, drying brown, persistent, splitting at base, the apex intact. LEAVES erect-spreading; petioles 28–45 cm long, 4–7 mm diam., terete, heavily tinged red-violet in early stages; geniculum 2.3–2.5 cm long, weakly sulcate; blades broadly ovate to rounded, moderately thick, gradually long-acuminate at apex, deeply lobed at base, 20–44 cm long, 15.5–29 cm wide, broadest at point of petiole attachment or slightly above; anterior lobe 15–29 cm long, the margins rounded; posterior lobes 7–15 cm long from apex of sinus to outermost point; sinus obovate to campaniform, sometimes closed, acute at apex; both surfaces matte to semiglossy, lower surface much paler; midrib convexly raised above, flat at apex, acutely raised below; basal veins 4–5 pairs, first and second free, third to fifth coalesced 2.5–3 cm, raised in valleys above, raised below; posterior ribs ± straight, inner margins sharply rolled up; primary lateral veins 4–6 per side, departing midrib at 40°–50° angle, curving toward apex and joining collective vein, sunken above, raised below; interprimary veins flat above, prominulous below; lesser veins scarcely visible; collective vein arising from the first basal vein, sunken above, raised below, 7–12 mm from margin. INFLORESCENCE erect-spreading, shorter than leaves; peduncles 18–20 cm long, 4–5 mm diam., terete, green heavily tinged with red-violet, one third to one half as long as petioles; spathe coriaceous, green tinged with red-violet, broadly lanceolate, 7.5–9 cm long, 2.5–3 cm wide, broadest at base, acuminate at apex, subcordate at base, inserted at 45° on peduncle; stipe 2–2.5 cm long in front, 1.5–1.8 cm long in back, 5 mm wide, green tinged with red-violet; spadix green (B & K Yellow-green, 6/7.5), 8–8.2 cm long, 1.2–1.5

cm diam. at base, 7–9 mm diam. at apex; flowers rhombic to 4-lobed, 3–3.2 mm long, 4–4.5 mm wide, the sides sigmoid; ca. 5 flowers visible in the principal spiral, ca. 7 flowers visible in the alternate spiral; tepals matte, weakly punctate, densely and minutely papillate, lateral tepals ca. 2.3 mm wide, the inner margin straight; pistils emergent, weakly raised, green; stigma linear, nearly obscure; lateral stamens emerging from base to apex, rapidly followed by third and fourth, exserted on short, translucent filaments; anthers yellow, ca. 0.5 mm long, 0.3 mm wide, held in a contiguous circle over pistil then retracting and opening at edge of tepals; thecae ellipsoid, scarcely divaricate; pollen yellow, fading to white. INFRUCTESCENCE pendent; berries dark orange, ovoid, 1.2–1.5 cm long, 1.2–1.4 cm diam., rounded at apex with 4 faint ridges; seeds 2, green, 1–1.3 cm long, 7–8 mm thick, markedly flattened on one side. Figs. 222 and 223.

Anthurium yetlense is endemic to Mexico in the Sierra de Juárez in northern Oaxaca. It is known only from the area south of Valle Nacional from 600 to 1,500 m in wet cloud forests.

The species is a member of section *Belolonchium* and occurs with and is similar to *A. umbrosum*. Both species are terrestrial; however, *A. yetlense* differs from *A. umbrosum* in that the inflorescence is much shorter than the leaves and the leaf is broadly ovate rather than ovate-triangular. The spadix of *A. yetlense* is green at anthesis whereas the spadix of *A. umbrosum* becomes violet-purple.

MEXICO. OAXACA: near Yetla (San Mateo Yetla), *MacDougall 410* (MEXU); between Valle Nacional and Oaxaca, W of Valle Nacional, *Croat 39768* (MO).

SPECIES EXCLUDED

Anthurium eggersii Engler. This species is a distinct species known only from Pacific Coastal Ecuador. Croat and Baker (1979) in the treatment of *Anthurium* for Costa Rica considered the species a synonym of *A. paludosum*, but further investigations show it to lack the entire cataphylls so characteristic of *A. paludosum*.

Anthurium crassinervium (Jacq.) Schott. This species is restricted to the Coastal Cordillera of Venezuela. Specimens cited as this species are *A. salviniae* or *A. schlechtendalii*.

Anthurium fraternum Schott. This species is restricted to northern Colombia in the mountainous region south of Santa Marta. Material with which it has been confused in Central America belongs to *A. huixtlense*.

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BIOGEOGRAPHICAL RELATIONSHIPS BETWEEN TEMPERATE EASTERN ASIA AND TEMPERATE EASTERN NORTH AMERICA: THE TWENTY-NINTH ANNUAL SYSTEMATICS SYMPOSIUM[1]

The Twenty-ninth Annual Systematics Symposium was held at the Missouri Botanical Garden in St. Louis on 23–25 September 1982 and consisted of two days of contributed papers and one day of invited papers. All previous meetings in this popular symposium series have been one-day symposia, each with a program of invited speakers. The primary reason for the change of format this time was to take advantage of the presence at the symposium of a large delegation of Asian botanists, especially the large group (16) from the People's Republic of China. Because this was the largest delegation of Chinese botanists to attend a scientific conference in the United States since 1949, it was an excellent opportunity for all participants to exchange ideas and information and to renew or establish contacts for cooperative scientific research and interchange.

The close relationship between temperate eastern Asia and North America is a classical topic in biogeography. The striking biological similarity between the two continents was first commented upon by Linnaeus in 1750 and was later, beginning in 1850, much elaborated upon by Asa Gray. The papers presented in this symposium provide a broad review of the geological, paleontological, zoological, and botanical aspects of the problem. Both classical and cladistic methods were used to analyze these biogeographical relationships. A special effort was also made to present a broad overview of the vegetation of China.

Invited speakers were the following: Daniel I. Axelrod, University of California, Davis; Margaret B. Davis (evening speaker), University of Minnesota; Warren Hamilton, U.S.D.I., Geological Survey; Hou Xue-yu, Institute of Botany, Beijing; Jen Hsü, Institute of Botany, Beijing; Malcolm C. McKenna, American Museum of Natural History; and Wu Zheng-yih, Institute of Botany, Kunming.

Because of the length of this symposium, it is

[1] Preliminary arrangements for this symposium, and particularly for the participation of the delegation of Asian botanists, were made by an organizing committee comprised of B. Bartholomew, University of California, Berkeley (currently California Academy of Sciences); D. E. Boufford, Harvard University Herbaria; G. Davidse, Missouri Botanical Garden; P. H. Raven, Missouri Botanical Garden; and S. A. Spongberg, Harvard University Herbaria. D. I. Axelrod (University of California, Davis), D. E. Boufford, G. Davidse, and S. A. Spongberg reviewed and did preliminary editing of many of the manuscripts in these proceedings, and R. Laurie Robbins (Missouri Botanical Garden) assisted with additional preliminary editing. The contribution of these people to the success of the symposium and to the publication of the proceedings is gratefully acknowledged. The Vegetation Map of China (1:1,400,000) that accompanies these proceedings was prepared by and is reprinted with permission from Hsioh-Hu Hou (Hou Xue-Yu), Institute of Botany, Academia Sinica, Beijing, People's Republic of China.—Nancy R. Morin, editor.

being published in two parts. The second part will appear in the following issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN.

This symposium was supported by National Science Foundation Grant DEB 78-10180. In addition, Mark Twain Bancshares and anonymous donors helped defray travel expenses.

Gerrit Davidse, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

NOTE ADDED IN PROOF: Since this symposium issue went to press, an extremely important paper by Zhang et al., which discusses the complicated tectonic evolution of China, appeared. The complete reference is: Zhang, Zh. M., J. G. Liou, and R. G. Coleman. 1984. An Outline of the Plate Tectonics of China. Geological Society of America Bulletin 95:295–312. Reprints may be obtained from the authors, Department of Geology, Stanford University, Stanford, California 94305.

EASTERN ASIAN–EASTERN NORTH AMERICAN PHYTOGEOGRAPHICAL RELATIONSHIPS—A HISTORY FROM THE TIME OF LINNAEUS TO THE TWENTIETH CENTURY[1]

D. E. BOUFFORD AND S. A. SPONGBERG[2]

ABSTRACT

The awareness and study of eastern North American–eastern Asian plant disjunctions is traced from the time of Linnaeus to the beginning of the twentieth century. Thomas Nuttall's previously overlooked contribution to this topic is discussed, and an annotated appendix of the taxa that he attributed to eastern Asia and North America is presented. Charles Darwin's influence on the thoughts and writings of Asa Gray is also discussed, based on published and unpublished letters and manuscripts in the Archives of the Gray Herbarium of Harvard University; the role that this correspondence played in the development of Gray's phytogeographical ideas and Darwin's theory of evolution is considered. A brief summary of the writings of Adolf Engler, and other nineteenth century botanists, pertaining to these disjunctions and their bearing on an understanding of vegetational patterns in the northern hemisphere is also given. The significance of the late nineteenth century explorations in China in making known the full extent of disjunctions between eastern Asia and North America has provided the basis for further work beyond the exploratory and theoretical stages of this fascinating pattern of plant disjunction.

The discontinuous distribution of the same or closely related taxa of plants between eastern North America and eastern Asia is but one of several patterns of disjunction that become evident when the flora of the temperate Northern Hemisphere is considered (Raven, 1972; Thorne, 1972; Wood, 1972; and others). Many of these patterns have been termed Tertiary relict disjunctions. Of these, however, the "classic" eastern North American–eastern Asian pattern is undoubtedly the best known and most often cited example of the disjunct occurrence of closely related taxa on two continents separated by thousands of kilometers. Despite the fact that most of the shared taxa in the two regions have been shown to be distinct from one another (the relationships are primarily closely related species of the same genus, or closely related genera of the same family), other factors noted by biogeographers that have strengthened the impression of a biological connection between the two regions are climatic and ecological similarities. The similarities of the forests of Japan, central China, and the southern Appalachians in appearance as well as in ecological associations are in many instances so great that a sense of déjà vu is experienced by botanists of one of the regions visiting the other.

Another important factor that has served to emphasize the floristic relationships between eastern North America and eastern Asia is the fact that this particular disjunction pattern was the first to be recognized by botanists. Moreover, the discovery and significance of this pattern figured in the discussions surrounding Darwin's theory of evolution, and it has been discussed not only by plant geographers but by botanical and scientific historians as well. The purpose of this paper is to trace briefly the historical aspects of the recognition of this distribution pattern and the accumulation of facts pertaining to it, and to summarize the major contributions to the study of this pattern that have been made from the time of Linnaeus to the beginning of the twentieth century. Special mention of the contribution and observations of Thomas Nuttall is in-

[1] We thank M. Byrnes for her help in the preparation of the manuscript, O. T. Solbrig, Director of the Gray Herbarium, for allowing access to the Darwin and Gray material in the Archives of the Gray Herbarium, and L. McWood, Archivist, for her patience and helpfulness. We also thank D. Kohn, B. G. Schubert, and P. F. Stevens for reading the manuscript and for their comments, and P. H. Raven, who suggested that we attempt this contribution. Lastly, we are grateful to B. Bartholomew and the library of the California Academy of Sciences for providing a copy of Miquel's paper of 1868, and to P. H. Raven and the Missouri Botanical Garden for providing copies of other literature that we were lacking.

[2] Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

cluded inasmuch as his penetrating insights into the relationships between the eastern Asian and eastern North American floras, as well as his phytogeographical observations, have to our knowledge hitherto passed unnoticed.

Early Recognition of the Floristic Similarities between Eastern North America and Eastern Asia—The Linnaean Era

The history of the early recognition of the floristic similarities between eastern Asia and eastern North America has been well outlined by Graham (1966, 1972b) and Li (1952, 1955). While credit for the discovery of the floristic relationships has frequently been given to Asa Gray, it was pointed out by M. L. Fernald (1931) that the first published reference to these similarities appears in a Linnaean dissertation, *Plantae Camschatcenses Rariores,* that was published in 1750 by Linnaeus's student, Jonas P. Halenius. As discussed by Graham (1966), the dissertation, including the listing of nine species then thought to occur in both Kamchatka and North America, was probably written by Linnaeus himself and not his student, who was apparently only required to defend the dissertation in Latin.

In 1751, the year after the initial publication of Halenius's dissertation, Pehr Kalm, another Swedish botanist, who had traveled extensively in North America during the years 1747 to 1749, published a "Short Account . . ." (see Larsen, 1939) of the plants he had collected in North America, seeds of which he had taken back for culture in Swedish gardens. In both this publication and in his *Travels into North America* (published in Swedish in the years 1753 to 1761, appearing in a first English edition in 1770), Kalm mentioned ginseng (*Panax quinquefolium* L.) and noted that it also grew in China and Korea. Kalm also noted the reputed medicinal value attached to the plant by the Chinese and recounted that the French collected the plant in Canada for export (via France) to China.

The dissertation defended by Halenius was reprinted in 1751 and again in 1787 (Graham, 1966); this last edition utilized Latin binomials and appeared three years after Thunberg's *Flora Japonica* (1784) had been published. Thunberg, also a student of Linnaeus but by 1784 an established botanist and explorer in his own right, also made brief mention in the Preface to his flora that many Japanese plants also occurred in Europe, America, and the East Indies, but particularly in the northern and adjacent, vast Chinese region. Among the plants treated are several that give direct evidence that Thunberg considered some plants in Japan and North America to be the same. Included in this group are:[3]

Sanicula canadensis L.
Viburnum dentatum L.
Sambucus canadensis L.
Lilium canadensis L.
Lilium philadelphicum L.
Aesculus pavia L.
Saururus cernuus L.
Asarum canadense L.
Asarum virginicum L.
Juglans nigra L.
Arum dracontium L.
Arum triphyllum L.
Magnolia glauca L.
Clematis virginiana L.
Teucrium virginiana L.
Bignonia catalpa L.
Juniperus virginiana L.
Pinus strobus L.
Amorpha fruticosa L.
Adiantum pedatum L.

No comments were made by Thunberg in the text mentioning that these species also occurred in the American flora, but all had originally been described from North America. In three instances he provided keys to separate Japanese from American species. Thus *Acer dissectum* Thunb. is distinguished from *A. negundo* L., *A. trifidum* Thunb. is separated from *A. pensylvanicum* L., and *Spiraea callosa* Thunb. is contrasted with *S. tomentosa* L.

There is no evidence that Thunberg was aware of the Halenius dissertation, but the next botanist to comment on the floristic affinities between the two regions was not only aware of Thunberg's *Flora Japonica* but compared it with Gronovius's (1739, 1743) *Flora Virginica.* Luigi Castiglioni used a comparison of these two floras as evidence of the similarity of the climates of the two regions in his two volume work, *Viaggio negli Stati Uniti,* that was published in Milan in

[3] The nomenclature and taxonomy follows Thunberg. No attempt has been made to give modern names that apply to these plants in both regions today, but many are obvious.

1790, three years after his return to Italy from the United States, where he had spent three years (1785–1787) traveling. In the account of his travels in the United States, he noted the affinities of many American plants, which he had observed growing, with those of Japan. In the second volume (p. 156) he wrote, "It is moreover to be observed that the plants are very similar to those of the eastern coast of northern Asia, the Magnolia, Illicium, Calycanthus, Ginseng and many others, for example, growing here as in Japan and China, thus confirming the assertion of Franklin that the eastern coasts of the old and new continents bear much analogy in their climates." The second volume concluded, moreover, with a lengthy section (pp. 169–402) entitled "*Osservazioni sui Vegetabili piu utili degli Stati Uniti*" in which numerous North American species were described with notes on their distribution and uses.

Castiglioni's work appeared in a German translation in 1793, and the original Italian edition was apparently reissued in 1845 (Stafleu & Cowan, 1976). It remained, however, for C. E. Faxon (1891) to point out the significance of Castiglioni's observations in relation to the biogeographical relationships between Asia and North America. Faxon's appreciation of Castiglioni's work also remained relatively unknown until Li (1955) rediscovered it, after his 1952 survey of the history of the recognition of the relationships had been published.

FREDERICK PURSH

Frederick Pursh (1814) was apparently the next botanist to comment on eastern North American–eastern Asian floristic relationships. Pursh's contribution to the knowledge of plant disjunctions between eastern North America and eastern Asia, however, was relatively slight and primarily limited to the single sentence describing the Pallas herbarium, which was quoted by Constance (1972) and is repeated here: "This extensive collection, now in the possesion of A. B. Lambert, Esq., was highly useful to me, in comparing the plants of North America with those of the north of Asia, to some of which they have great affinity, and others are common to both continents." The few other instances where Pursh made note of eastern Asian–eastern North American disjuncts in his *Flora* are indicated in Appendix 1.

THOMAS NUTTALL

In twentieth century reviews of early botanical literature dealing with the disjunct distribution of plants between eastern Asia and eastern North America, Asa Gray has generally been given the major share of the credit for being among the first to point out this pattern (Fernald, 1931; Hara, 1952, 1972; Li, 1952; Graham, 1972; Good, 1974). Because of the detail of Gray's (1840, 1846, 1856, 1857, 1859) studies, the attention they received at the time, and their contemporary importance in relating to Darwin's ideas on evolution, Gray has also been credited with being among the founders of the field of biogeography (Good, 1955; Li, 1952). The few papers that preceded Gray's (Halenius, 1750; Thunberg, 1784; Castiglioni, 1790; Pursh, 1814) were in no way as detailed, nor as critical in their analysis of this pattern of disjunction as was his "Diagnostic Characters" paper of 1859. Each of these papers tended to point out that some of the plants from North America were the same as plants in distantly separated parts of the world, particularly those in eastern Asia. None of them discussed the implications of populations of a single species being so widely separated and, with botany in most of the Northern Hemisphere still in the exploratory stage and with vast areas still botanically unknown, it is unlikely that they should have. The explorations that continued through the early part of the 1800s in the American West, in eastern Asia, in Canada, and in other parts of the world led to the discovery of large numbers of new species and made available numerous specimens to help fill in gaps in plant distributions. The floristic works mentioned above that were based on these explorations took into account specific geographical regions and were often based on very limited numbers of specimens so that it was difficult to make direct comparisons with other parts of the world except through the literature. Even so, the influx of specimens contributed to the growth of the large private herbaria that were acquiring specimens at the time and eventually made possible the kinds of comparisons of the world's flora made by Gray.

One exceptional work, however, that preceded Gray's papers, and one that has apparently been overlooked despite its importance to North American taxonomy, is Thomas Nuttall's (1818) *Genera of North American Plants.* Nuttall's *Genera* was the culmination of nearly ten years' study of the plants of North America, particularly those

of the area that was then the United States and its territories. Nuttall was unusually well prepared to write the *Genera* for he was equally familiar with many North American plants in the field and in the herbarium, and had become familiar with others that were growing in the gardens of Philadelphia, particularly those in Bartram's Garden (Graustein, 1967). His studies before writing the *Genera* included field work across much of the northern United States from the East Coast nearly to the Rocky Mountains, travel down the Mississippi River to New Orleans, field work in the eastern coastal region, especially around Philadelphia, short excursions into New York state and into Canada around Niagara Falls, and a fairly long trip through the southeastern United States that retraced parts of the routes of several earlier botanical explorers including those of Bartram and Michaux (Graustein, 1967; Pennell, 1936). From the time of his arrival in Philadelphia in the spring of 1808 Nuttall had ready access to the largest herbaria in the United States through his connection with Benjamin Smith Barton and other Philadelphia botanists and was later able to study specimens in the large private herbaria in England before preparing his *Genera.*

Nuttall was also apparently aware of the works of earlier and contemporary botanists. In the introduction to the *Genera* he stated that he relied heavily on Pursh's (1814) *Flora of North America,* for which he considered his *Genera* as "supplementary"; Sprengel's (1802) *Introduction to the Study of Botany,* whose style he followed for the description of genera; and on Jussieu's (1789) *Genera Plantarum,* whose inclusion of notes on habitat for each genus he followed. Although Nuttall argued strongly for a classification in which genera were arranged according to their natural affinities, he followed the Linnaean sexual system, which was in use in the United States at the time, although he did comment on the natural relationships of several genera. Nuttall was apparently able to determine the worldwide distribution of North American genera during a stay in England after his long collecting expedition up the Missouri River with the Astorians in 1811. He had planned only a short visit to England after his trip to the American West in 1810 and 1811 (Graustein, 1967), but it was more than two years before he could return to the United States for he was caught in England when the War of 1812 broke out. He made good use of his time by contacting the leading botanists in England and in examining the holdings of Joseph Banks's and A. B. Lambert's herbaria; the latter herbarium contained specimens collected by Pallas in Siberia and eastern Asia. Nuttall's familiarity with the plants of the northern United States and the chance to examine specimens in the Lambert and other herbaria, where he no doubt saw many North American plants that were still unknown to him, prepared him well for a trip to the southeastern United States when he returned to Philadelphia in 1815. He was able to retrace the routes of many of the first botanical collectors to that part of the country as he traveled through the mountains of Virginia, Kentucky, Tennessee, and the Carolinas and across the Piedmont and Atlantic Coastal Plain provinces of the Carolinas and Georgia (Graustein, 1967). Nuttall was also able to examine specimens in the herbaria of several noted contemporaries who lived in that part of the country and saw additional plants from the southeastern United States in their collections. One particularly useful collection was that of William Baldwin, who had collected specimens in western Florida during two years spent there while in the Navy (Graustein, 1967). Following these field and herbarium studies, Nuttall spent most of the years 1816 and 1817 writing the *Genera,* which was published in 1818 (Pennell, 1936).

The most important aspect of the *Genera* from a phytogeographical standpoint was Nuttall's inclusion of comments on "A view of the geographic distribution of each genus . . . , not always sufficiently accurate for the existing state of the science, and the rapid progress of modern discovery" (Nuttall, 1818, p. vii). These "views" on geographic distribution were Nuttall's attempt to explain the relationships and distribution of North American plants on a worldwide scale.

Nuttall mentioned the geographical range and made other comments for each genus he treated. While he did not limit his observations to plants exhibiting an eastern Asian–eastern North American distribution, the comments of interest to us here are those that pertain to that pattern and show that Nuttall was aware of a phytogeographical connection between the two regions. In some cases Nuttall merely stated that a particular North American genus was also found in eastern Asia (here taken to include the Indian subcontinent and the Himalayas), but in other cases it seems clear that he was well aware of the significance of disjunction between the two widely sep-

arated regions. Nuttall's comments (pp. 274, 275) under *Chimaphila,* a genus in which he recognized two species, *C. umbellata* and *C. maculata,* are especially insightful: "Indigenous also to the North West Coast of America.—Menzies. Probably both species of the genus will be found also in East Asia and Europe." The prediction that plants peculiar to one of these regions might be expected in the other was later made by Gray (1859, p. 416) and discussed by Wood (1972), but the fact that Nuttall had earlier suggested this has apparently been overlooked.

Although Nuttall did not restrict his comments to plants in those two geographical regions, we have listed in Appendix 1 examples from the *Genera* where he indicated disjunction between eastern North America and eastern Asia. The few instances where Pursh (1814) had previously commented on the same genera are also indicated. It must be remembered that taxonomic concepts of the early 1800s were different from our own. Nevertheless, Nuttall's ideas on phytogeography and the relationships of the North American flora were remarkably modern in many respects and deserve to be accorded their rightful place in the progression of knowledge of plant geography. Nuttall has yet to receive the credit he is due for the phytogeographical significance of his work, and none of his many biographers (Anonymous, 1860; Beidleman, 1960; Durand, 1860; Ewan, 1971; Graustein, 1967; Jones, 1937; Pennell, 1936; Smith & Thieret, 1959; Stuckey, 1968) have mentioned it. We hope that by indicating these examples of his awareness and interest in plant distributions that future biogeographers will acknowledge particularly his contribution to the study of eastern North American–eastern Asian plant disjunctions.

ASA GRAY

As indicated above, Asa Gray was not the first botanist to point out the relationships of the eastern North American and eastern Asian floras, but Gray's series of papers on this topic did focus scientific attention on this disjunct distribution pattern. Moreover, Gray fully examined and analyzed the problem utilizing the materials available to him and in so doing laid the foundation on which future work was possible. Gray's hypothesis of the causes of the eastern North American–eastern Asian disjunctions, moreover, brought the observed pattern into the scientific realm of biogeographic discussion and analysis on a multidisciplinary level.

The first evidence that Gray was aware of the relationship appeared in his reviews (1840, 1846; see Graham, 1972a, b, and Stuckey, 1978, for reprintings) of Siebold and Zuccarini's *Flora Japonica* and *Florae Japonicae Familiae Naturales,* in both of which he listed genera and species that were either similar, or common in both eastern North America and Japan. Gray apparently put aside this topic for about ten years, since the next mention he made of the relationship in print was in 1856 in the preface to his list of determinations of specimens collected in Japan by S. W. Williams and J. Morrow. Both of these men had been attached to Perry's expedition to Japan and the China seas. In his introductory remarks, Gray again mentioned the floristic relationships and indicated that he hoped to comment on them again once Charles Wright's collection of Japanese plants had been studied and named. Wright had been one of the botanists on the North Pacific Exploring Expedition under the command of Commodore Rogers and had returned home in 1856, during the time that Gray was involved in the preparation of his "Statistics of the Flora of the Northern United States." It was in this paper (1856, 1857) that Gray laid the framework of comparison that he was to utilize again in his now classic paper (1859) based on Wright's collections.

It is of interest to note that Gray had previously received and reviewed (Gray, 1854) J. D. Hooker's dissertation concerning the New Zealand flora (Hooker, 1853), which had been published in 1853 as an "Introductory Essay" to his *Flora Novae-Zelandiae.* The format of that essay in comparing the distribution and affinities of New Zealand plants was basically the same that Gray followed in his "Statistics" and "Diagnostic Characters" papers. It is also of interest to note that in his introduction Gray mentions that he was "requested by an esteemed correspondent . . . to exhibit, in a compendious and convenient form, the elements of the flora I was occupied with." The esteemed correspondent, was, without any doubt, Charles Darwin, with whom Gray had begun to correspond in 1855,[4] and whom he

[4] Darwin's letters to Gray are preserved in the Archives of the Gray Herbarium of Harvard University, but most have been published. Likewise, many of Gray's letters to Darwin, the originals of which are preserved in the Cambridge University Library, have also been published. See Historical Records Survey (1939); J. L. Gray (1893); and F. Darwin (1887, 1903).

mentions elsewhere in the "Statistics" paper. From reading Darwin's letters to Gray during the period 1855 to 1859, and from studying and comparing Hooker's New Zealand essay with Gray's subsequent papers, one is given the distinct impression that Darwin's questions and suggestions prodded Gray into action, and that Darwin's and Hooker's ideas strongly influenced Gray's thinking concerning the geographic affinities of the North American flora and the analysis of these relationships.

In his response (22 May 1855) to Darwin's first letter, Gray wrote that he ". . . had already intended, when the Flora of N. America should be finished to work up the geographical and climatic relations of this flora, and to compare it critically with the N. European and N. Asiatic floras." He continued by stating that he welcomed Darwin's questions, "and, if you will kindly give me hints as to what is needed, and how to do it, I will undertake the comparison of the plants of this moderate area (bounded by the Atlantic Coast, New Brunswick, St. Laurence, Great Lakes, Mississippi, and Potomac or Chesapeke Bay) with the General N. Amer. flora and with that of the northern part of the Old World, and print the result either in the volume itself,[5] or in some Journal, as you suggest. So, you see, far from taking your suggestion amiss, I respond to it by asking you to tell me very particularly how to do it, so that it may be of use."

In his second letter to Gray (8 June 1855) Darwin asked specifically concerning the geographical distribution of North American plants and their affinities and total ranges. Darwin wrote, "The ranges of plants, to the East and West, viz. whether most are found in Greenland and Western Europe, or in E. Asia appear to me a very interesting point as tending to show whether the migration has been Eastward or Westward," and he expressed pleasure that Gray was thinking of "drawing up some notice on geographical distribution . . . ."

In his third letter to Gray (dated 2 May, probably 1856?) Darwin wrote, "I would give a list of temperate plants, if any, found in Eastern Asia, China, and Japan, and not elsewhere. Nothing would give me a better idea of the Flora of U.S. than the proportion of the genera to all the genera, which are confined to America, and the proportion of genera confined to America and Eastern Asia with Japan; the remaining genera would be common to America and Europe and the rest of the world; I presume it would be impossible to show any especial affinity in genera . . . between America and *Western* Europe; America might be related to Eastern Asia, (always excluding Arctic forms) by a genus having the *same* species confined to these two regions; or it might be related by the genus having different species, the genus itself not being found elsewhere."

After receiving "sheets" of the first section of Gray's "Statistics" paper, Darwin wrote (12 October 1856) that nothing had surprised him more than the greater generic and specific affinity between the eastern North American flora and the eastern Asian flora, an affinity greater than that between the eastern and western American floras, and he asked if climate explained this affinity or was it one of the "many utterly inexplicable problems" of botanical geography. In another, undated letter written in 1857, Darwin requested Gray to contribute further to geographical problems despite the fact that Gray complained of his incomplete knowledge of plant distribution. Darwin urged Gray to prepare reports as the work progressed, and wrote, "So do pray look at this side of the question, and let us have another paper or two like the last admirable ones."

While Gray did mention the relationships between eastern North America and eastern Asia in his "Statistics" paper, these relationships were not developed fully, undoubtedly reflecting the fact that those comparisons he did make were based on literature reports and only a relatively few specimens. Thus, in a section dealing with widely dispersed species that "reappear in Japan, the Himalaya, or some part of northern Asia, but are not European," Gray listed only the following 13 species: *Brasenia peltata* Pursh, *Sium lineare* Michaux, *Cryptotaenia canadensis* (L.) DC., *Heracleum lanatum* Michaux, *Osmorhiza longistylus* (Torrey) DC., *Aralia quinquefolia* (L.) Decaisne & Planchon, *Viburnum lantanoides* Michaux, *Monotropa uniflora* L., *Phryma leptostachya* L., *Smilacina trifolia* (L.) Desf., *Trillium erectum* L. var., *Camptosorus rhizophyllus* (L.) Link, and *Adiantum pedatum* L. By 1859, however, Gray had had the opportunity to study and name the rich collections of Charles Wright from Japan, and the list of shared species between eastern North America and Japan alone included 134 species! Gray now had the speci-

[5] The volume referred to by Gray was the new, second edition of his *Manual of Botany of the Northern United States* on which he was then working.

mens that would allow for the floristic comparison with eastern Asia that Darwin had requested in his second letter.

Gray's (1859) published analysis of Wright's Japanese collection took the form of an essay in which he compared the Japanese flora with the North American and other north temperate floras. In it Gray described only the new taxa from among Wright's collections (these proposed in footnotes), indicating (p. 377) that a detailed account of the entire collection was ". . . intended to form a part of Mr. Wright's general report upon the extensive and interesting botanical collections made by him during the whole cruise of the Expedition. As this report, and that of the important scientific results of this Expedition in various other departments, may not be published for some time, I am permitted and requested, by the Commander of the Expedition, —ever considerate of the interests of science, —briefly to make known the principal novelties which have been discovered in this field. The discoveries . . . also relate to the detection of known species in a region where they were not known before, and to the identification and elucidation of many obscure species. It will be best, therefore, to take a cursory general notice of the more interesting plants of this collection, adding any remarks which it may be worth while now to make upon their geographical distribution of their characters, and appending the diagnoses of new genera and species in the form of foot-notes."[6]

It is both in the text of the essay (where he elucidated previously described species and communicated his observations on the similarities of Japanese and other north temperate plants) and in the discussion of his "Tabular View of the Distribution of Japanese Plants and Their Nearest Allies in the Northern Temperate Zone" (pp. 424–436) that the disjunct distributional pattern between eastern North America and eastern Asia (Japan) became vividly apparent. Some of Gray's comments and observations concerning this pattern and the floristic similarities are quoted here.

In the discussion of the Berberidaceae (pp. 380, 381) Gray wrote, "But perhaps the most interesting and most unexpected discovery of the expedition is that of two strictly Eastern North American species of this order, —each the sole representative of their genus, —viz. *Caulophyllum thalictroides*, and *Diphylleia cymosa*, of Michaux. . . . Supposing these two plants to be satisfactorily identified as to species,[7] are we to regard them as the descendants of a common stock, though now separated by one hundred and forty degrees of longitude? Or are we to suppose them independently originated in two such widely distant regions?" And in the discussion (p. 416) of his newly proposed genus *Heloniopsis*, Gray wrote, "It may be briefly described as a *Helonias* with few flowers, a single and slender style surmounted by a depressed-capitate stigma, and the seeds appendaged only at the hilum. Two things are noteworthy respecting this plant:—1. Its conformity to the rule, if it may be so called, that peculiar Eastern North American types have their counterparts in Japan. For the original and only true *Helonias*—one of the rarest plants in the United States—is found only in a few localities in New Jersey, the adjacent parts of Pennsylvania and Delaware, and in Virginia." Numerous other examples could be quoted, some dealing with identical species, others concerning closely allied species, or, as in the last example above, closely allied genera.

In his "Tabular View," Gray listed about 580 Japanese species "which have particular relatives in other and distant parts of the northern temperate zone" (p. 422), and listed in parallel columns the corresponding taxa represented in the floras of Europe; Central and Northern Asia; Western North America; and Eastern North America. Identical species shared between the flora of Japan and another area(s) were set in italic type. In analyzing this data, the following summary was presented (p. 437):

The whole number of Japanese entries is about 580
The whole number of Asiatic entries is about 44; in italics 274
The whole number of European entries is about 282; in italics 214
The whole number of W. American entries is about 216; in italics 162
The whole number of E. American entries is about 356; in italics 223

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[6] Gray's fears that the scientific results of the expedition might not be published were justified; the complete manuscript that he alluded to remains unpublished, but is preserved in the Archives of the Gray Herbarium of Harvard University.

[7] The Japanese and North American species of both *Caulophyllum* and *Diphylleia* were subsequently shown to be distinct.

Based on this analysis Gray was able to conclude (p. 437) that "It is intersting to notice that, notwithstanding the comparative proximity of Japan to Western North America, fewer of its species are represented there than in far distant Europe. Also, —showing that this difference is not owing to the separation by an ocean, —that far more Japanese plants are represented in Eastern North America than in either. . . . If we regard the identical species only, in the several floras, the preponderance is equally against Western as compared with Eastern North America, but is more in favor of Europe. For the number of species in the Japanese column which likewise occur in Western North America, are about 120; in Eastern North America, 134; in Europe, 157." But, considering the overall similarity at all levels, Gray concluded that of the 580 Japanese entries, 48 percent have corresponding European representatives and 27 percent are identical species; the comparative figures for western North America were calculated as 37 percent for corresponding taxa and 20 percent for identical species, while for eastern North America, the percentage of corresponding taxa was an overwhelming 61, and that for identical species was 23.

In summarizing the floristic data that he had presented concerning the New Zealand flora and its affinities with the floras of Australia and Tasmania and temperate South America, Hooker (1853, p. xxxvi) wrote that "Enough is here given to show that many of the peculiarities of each of the three great areas of land in the southern latitudes are representative ones, effecting a botanical relationship as strong as that which prevails throughout the lands within the Arctic and Northern Temperate zones, and which is not to be accounted for by any theory of transport of variation, but which is agreeable to the hypothesis of all being members of a once more extensive flora, which has been broken up by geological and climatic causes." It was with a quotation of this passage that Gray concluded his review of Hooker's essay in 1854, and in attempting to explain the disjunct occurrence of identical species and the otherwise strong floristic affinities between the Japanese and eastern North American floras, Gray built a similar argument to explain the observed facts.

Gray wrote (1859, p. 440), ". . . it will be almost impossible to avoid the conclusion, that there has been a peculiar intermingling of the Eastern American and Eastern Asian floras, which demands explanation." On page 444 he wrote, "The discovery of numerous closely related species thus divided between two widely separated districts might not, in the present state of our knowledge, suggest former continuity, migration, or interchange; but that of identical species peculiar to the two inevitably would." Gray suggested further (p. 442) that the interchange between "the temperate floras of the western part of the Old World and the New had taken place *via* Asia," an idea that he attributed to Bentham. Gray (1859) credited Bentham with pointing out that interchange between *all* of the Old World, including western Europe, and the New World had taken place *via* Asia. Gray thought the statement may have been made in conversation or in correspondence between the two for Gray did not believe these thoughts had been published. Gray cited as evidence to support this theory the fact that such large North American genera as *Aster* L., *Solidago* L., and *Eupatorium* L. (Compositae), *Euphorbia* L. (Euphorbiaceae) and *Solanum* L. (Solanaceae) "... are represented in eastern Asia by a small number of species, which gradually diminish or altogether disappear as we proceed westward toward the Atlantic limits of Europe, whilst the types peculiar to the extreme west of Europe (excluding of course the Arctic flora) are wholly deficient in America." Bentham (1858, p. 35), in his "Synopsis of the genus *Clitoria,*" had indeed published his view that there had at one time been an "ancient continuity of territory between America and Asia, or at any rate with a climate more meridional than would be effected by a junction through the chains of the Aleutian and Kurile Islands."

It should be recalled that Gray was writing just prior to the publication of Darwin's (1859) *Origin of Species,* although Gray was aware of Darwin and Wallace's (1858) joint presentation to the Linnean Society and indicated his acceptance of their views (p. 443, in footnote). Moreover, Darwin and Gray had carried on a constant and frequent correspondence during the period prior to the publications of Gray's "Diagnostic Characters" (see Good, 1955). Darwin had tested many of his ideas on Gray, anxious for both more data to test his hypotheses and Gray's reactions based on his knowledge of the American flora. Considering the influence of both Darwin and Hooker, it is perhaps not surprising that Gray concluded his analysis of Wright's Japanese collections with an attempt to explain the revealed disjunctions

utilizing paleobotanical evidence and geological and glacial history (as they were then understood) coupled with an "evolutionary" outlook that embraced "common descent." Thus, the concept of a disrupted, once more widely distributed North Temperate flora was proposed as a working hypothesis to explain the observed facts. Gray had not only succeeded in fully pointing out the floristic similarities between eastern North America and eastern Asia, but he had (with due credit to Darwin, Hooker, and his geologist friend and colleague, Professor J. D. Dana) also proposed the working hypothesis of the causes—a hypothesis that remains valid in many ways today.

Gray's hypothesis gave support to Darwin's theory of evolution but refuted the theories of the Harvard naturalist, Louis Agassiz (Gray, 1860). Dupree (1959) has devoted several pages to the conflict between Gray and Agassiz and to the debate that both Gray's "Diagnostic Characters" and Darwin's *Origin* excited. That Gray's paper and Gray's influence surrounding the acceptance of Darwin's theories in North America were important undoubtedly brought Gray's "Diagnostic Characters" paper to the attention of a wider scientific public than might otherwise have been expected. It is understandable, therefore, that Gray has generally been considered the first botanist to recognize the eastern Asian–eastern North American pattern of disjunction.

The awarding of the major share of the credit to Asa Gray in connection with the floristic relationships between eastern North America and eastern Asia was also undoubtedly the result of Gray's continued interest in this phytogeographical distribution pattern and the published addresses concerning this topic that he delivered after the appearance of his "Diagnostic Characters" paper in 1859. Thus, in 1873, in his address to the American Association for the Advancement of Science (Gray, 1873a), Gray extended his floristic comparisons to include a broader region of Asia (Northeastern Asia, Japan to the Altai and the Himalayas) and to compare the relationships of this area with western North America (Oregon and California). In this paper Gray also appended a list of species common to the United States and Europe, a list which was later reprinted in England (Gray, 1873b). And in 1878, in a lecture presented to the Harvard University Natural History Society entitled "Forest Geography and Archeology," Gray outlined the similarities and dissimilarities of the forests of the temperate zone and compared those of the "Japan-Manchurian" region with those of Europe and eastern and western North America. In an effort to explain the similarities and dissimilarities he again emphasized that current distributions were the direct result of past history.

European Contemporaries of Gray

F. A. W. Miquel

Soon after the publication of Gray's "Diagnostic Characters," several European botanists turned their attention to the problem of the disjunct distributional pattern described by Gray, the affinities of the floras involved, and the hypothesis offered by Gray to explain biogeographical data. F. A. W. Miquel (1867a, b), a Dutch botanist, published two papers in 1867; one in which he discussed the affinities of the Japanese flora with that of North America (Miquel, 1867a), the other on the origins and phytogeographical relationships of the Japanese flora (Miquel, 1867b). While Miquel accepted the distributional pattern described by Gray and did not question the geological evidence of a once more widespread temperate flora in the Northern Hemisphere, he was unwilling to accept the Darwinian concept of common descent to explain the presence of "analogous" species in Japan and eastern North America. In his paper on the relationships of the Japanese flora with that of North America, Miquel tabulated 27 woody species common to Japan and all of North America, and 76 herbaceous species, not including analogous or similar species pairs. A year later (1868) he considered 81 species to be shared between eastern Asia and all of North America. While he agreed to the single (vs. the multiple) origin of a species, he maintained that the analogous species in each area were "created" independently and were not descendants from a common stock.

Adolph Engler

Aware of Darwin's, de Candolle's, Gray's, Hooker's, and Bentham's ideas and the work they had done in this area, Adoph Engler (1879) used evidence from a number of fields in his attempt to interpret the history of the world's vegetation since the Tertiary and to explain present-day distribution patterns. Engler was convinced that the distribution of extant plants was the result of disruptions in ranges, changes in climate, migration, and evolution, and he placed the greatest importance on past geological and climatic events as the causes. He believed that numerous extant

species had histories that extended back to the Tertiary, and he was aware that during the Tertiary the vegetation of the eastern part of North America extended westward at least as far as the Rockies and had occurred there into the Neogene. Engler cited fossil evidence based on the work of Lesquereux to support this hypothesis. He noted that many eastern North American taxa that were not now extant in western North America were represented there by fossils, but that only three western genera. *Prosopis* L., *Cassia* L., and *Ziziphus* Miller, were known as fossils in the East. Parallel forms in eastern and western North America were considered to be remnants of a once more widespread floristic element. Engler postulated that the Rockies had been lower in the past, the prairies less extensive, and that a mostly continuous, or at least similar, flora extended from the East to the West Coast, and that this flora became disrupted through a drying of the climate in the West, but evidence of a once more widespread flora still remained in such taxa as *Ptelea angustifolia* Bentham, *Aesculus californica* Nuttall, *Acer negundo* L. (as *Negundo californicum* Torrey & Gray), *Staphylea bolanderi* A. Gray, *Rhus diversiloba* Torrey & Gray, *Cercis occidentalis* Torrey ex Gray, *Amelanchier alnifolia* Nuttall, *Calycanthus occidentalis* Hooker & Arnott, *Rhododendron californicum* Hooker, and *Styrax californicum* Torrey (Engler, p. 12) in the West. All of these plants have disjunct counterparts in eastern North America.

Based on the paleobotanical studies of Heer, Engler cited fossil evidence of relatives of extant plants of Japan occurring on Sakhalin, and believed that the climate of Japan in the Miocene had been similar to that of present day southeastern Asia and supported a similar vegetation. He also felt that the knowledge of the Pliocene was insufficient and that a better knowledge of that period of time was necessary before a complete understanding of the history of the eastern Asian–eastern North American disjuncts could be obtained. Engler also lamented the fact that so little was known about the high mountains of China in a phytogeographical sense, especially since he was aware of the Japan-Himalayan-North American connection. He postulated that a rich Tertiary flora probably spread southward in China along the mountains that stretched from the Amur River region, around the Gobi Desert, to the Himalayas.

He gave examples of plants (*Liquidambar* L., *Platanus* L., *Ostrya* Scopoli, *Castanea* Miller) known as fossils in Europe, and believed that these genera had been richer in numbers of species, and were much more widespread in the past, as were many other genera now restricted to the warmer parts of North America and eastern Asia. Engler believed that the plants now restricted to eastern Asia and eastern North America had a much wider range, were even circumboreal, during the Tertiary because of a more widespread, equitable climate that prevailed then.

Another important aspect of Engler's work was that he pointed out that many of the eastern Asian–eastern North American disjuncts considered by Gray to be "identical" were already being shown to be distinct. He noted that Miquel (1868) had reduced Gray's (1859) list of 134 "identical" species to 81 taxa from Japan and North America that Miquel considered to be the same. Grisebach (1872, pp. 520–522, 602, 603), as pointed out by Engler, further reduced Miquel's list to only two examples, "*Elodea petiolata*" and *Carex rostrata* Stokes, of plants restricted to Japan and the eastern United States (21 plants were automatically excluded from consideration by Grisebach (1872) because they also occurred in Canada, and 41 were excluded on the basis of their occurrence in western North America). Engler (1879, pp. 25, 26), however, provided a list of 140 plants he considered to be shared between eastern Asia and North America, indicating the geographical region where each grew in the two regions. He also pointed out that the vast majority were forest plants, and only very few were found in open habitats. There are some errors in distribution data in the list, for example, *Coptis occidentalis* Torrey & Gray and *Mahonia aquifolium* Nuttall are both credited to Atlantic North America while *Melothria pendula* L. is credited to Pacific North America. In general, however, the list is more complete and refined than Gray's (1859) and indicates that many plants that Gray had considered to be identical are actually distinct.

In explaining the history of the world's vegetation Engler (1879) made considerable use of fossil evidence, especially of fossil floras in the arctic regions. He believed that the land surface had been lower between Europe and central Asia during the Tertiary and that the sea was not as great, perhaps resulting in a more equitable climate that accounted for both a widespread mixed mesophytic forest in present day arctic situations and the opportunity for an exchange of species across a bridge in northeast Asia–northwest North

America. Engler postulated that the plants now restricted to the two disjunct regions were once more widespread further north, "as the Arctic flora now is," and that they had migrated southward as the climate cooled. These plants mostly became extinct in western North America because of the markedly different climate there, but still occurred in Japan and eastern North America where the climates remained similar. Those plants that survived in the West underwent evolutionary change in response to different edaphic factors, thereby resulting in different species of "*Negundo*" Boehmer, *Rhus* L., *Cercis* L., *Osmorhiza* Rafinesque, and *Platanus* L. in the eastern and western United States. The less drastic climatic changes in Japan accounted for the relatively higher number of genera, particularly for the higher number of monotypic genera, surviving there. Engler was apparently the first to refer to extant floras whose members were abundantly represented by fossils from the Tertiary at high latitudes in the Northern Hemisphere as the "Arcto-tertiäre Element." The extant regions referred to by Engler as supporting this "Arcto-tertiäre Element" were eastern North America, eastern Asia (Himalaya, Japan, northern China), and south in the Andes. This reference to the Andes suggests that Engler recognized an eastern North American temperate element in the flora of Mexico and Central America. This is the first indication of an awareness of this additional pattern of disjunction, an awareness that has generally been credited to Watson (1891; see Graham, 1973).

The extension of the recognition of floristic affinities to a wider area of the Asian continent went hand in hand with the development of floristic knowledge of China and other areas of mainland Asia. Thus, by 1873 H. F. Hance, who had been occupied with Chinese plants for many years, was able to list 21 species of the Chinese flora that occurred or were represented by closely allied species in the Caucasus region of southern Europe and western Asia, a region now known to support a flora rich in examples of Arcto-Tertiary elements. The first installments of Forbes and Hemsley's "Enumeration of All the Plants from China . . ." appeared in 1886 and 1887, and in the systematic treatments the Chinese and extra-territorial distribution was given for each taxon. While this series was not completed until 1905, the wide circulation of the parts as they were published stimulated further collecting activity in remote areas of the Chinese interior (Thiselton-Dyer, 1905). The valuable collections made by Augustine Henry in central China were acquired by and distributed from the herbarium at Kew as a direct result of this stimulation. The continued discovery of botanical novelties in interior China, many of considerable botanical and horticultural interest, also increased interest in the botanical exploration of the Chinese empire. It was essentially in response to a strong desire to introduce these newly discovered ornamental species into cultivation in England that the Veitch nursery firm sent E. H. Wilson to China on two expeditions. Wilson not only carried on the work begun by Henry (and the earlier French missionaries), but brought the Chinese flora to the attention of late nineteenth and early twentieth century botanists.

Diels and the Flora of Central China

As mentioned above, the gaps in the flora of central China that had been noted by Engler (1879) began to be filled within a few years as the collections of French missionaries and other European botanists began to reach Europe. Enough new material had been amassed and new information made available since Engler's (1879) paper to enable Diels (1900–1901, 1905) to write a definitive work on "Die Flora von Central-China" in which he discussed the history of botanical exploration, the geography, ecology, vegetation, and the relationshps of the flora, in addition to providing a list of the known taxa. The area treated by Diels took in nearly all of the present-day province of Sichuan as well as the adjoining parts of the surrounding provinces. Coincidentally, this happens to be a region containing a large number of taxa with North American relatives. Diels's comparison of the flora of central China with those of other parts of the world showed that a greater number of taxa were shared with Japan to the east than with the much closer Himalayan region to the west, although the vegetation in central China and Japan was somewhat different (Diels, 1900–1901). Diels showed that the Asian distribution of the elements in the flora exhibiting disjunction between eastern Asia and North America could be categorized into four types: 1) genera with members reaching to Malesia; 2) genera reaching from the Himalayas to Japan; 3) genera reaching only to Japan; 4) genera restricted to central China and North America. Examples of each are: 1) *Arisaema* Martius, *Aletris* L., *Magnolia* L., *Schi-*

sandra Michaux, *Illicium* L., *Polygonum* L. sections *Cephalophilon* Meisner in Wallich and *Echinocaulon* Meisner in Wallich, *Vitis* L., *Parthenocissus* Planchon, *Gordonia* Ellis, *Nyssa* L., *Clethra* L., and Saururaceae; 2) *Phryma leptostachya* L., *Panax* L., *Adiantum pedatum* L., and several others; 3) *Caulophyllum* Michaux, *Hamamelis* L., *Stewartia* L., *Diphylleia* Michaux, plus others; 4) *Cypripedium arietinum* R. Brown, Calycanthaceae, *Liriodendron tulipifera* L., *Decumaria* L., and *Gymnocladus* Lamarck. Diels clearly based his classification of eastern Asian–North American disjunctions on the distribution of the Asian members of this pattern without regard to the distribution of the North American counterparts.

Mention must also be made of the *Forest Flora of Japan,* a volume Charles Sargent (1894) wrote after his first-hand observation of the Japanese flora during his journey there in 1892. Continuing in the tradition of Asa Gray, his mentor and friend, Sargent accounted for the ligneous flora of Japan and compared the genera with those that occur in eastern North America, essentially updating Gray's "Forest Geography and Archeology." Charles Sargent should also be given credit as one of the first Americans who realized that the climatic and floristic similarities between eastern Asia and eastern North America would allow for the successful cultivation of numerous Asian species in eastern North America. As first director of the Arnold Arboretum of Harvard University, Sargent had been successful with the cultivation of plants raised from seeds received from Emil Bretschneider, who was based at the Russian consulate in Peking, and immediately determined that the floristic exploration of China would not only result in furthering botanical knowledge of eastern Asia, but would also result in new ornamental plants for cultivation in America. To this end, Sargent engaged E. H. Wilson to collect specimens, seeds, and living plants in "western" China.

The history of the botanical exploration of China (for which see, in particular, Bretschneider, 1898) is not within the scope of this paper, but Wilson's activities both for the Arnold Arboretum and earlier for the Veitch Nursery firm in England during the period 1899 to 1910 greatly increased knowledge of the Chinese flora and extended the knowledge of the eastern Asian–eastern North American distribution pattern. Thus, Sargent (1913) was able in an Introduction to Wilson's *A Naturalist in Western China,* to compare the ligneous flora of North America with that of China, again pointing out the similarities but also noting the differences between the floras and emphasizing the richness of the ligneous flora of China. Further comparisons, particularly of the ligneous flora, were subsequently made by H. H. Hu (1935, 1936) and were the first contributions to the elucidation of this pattern of disjunction to be made by a Chinese botanist.

Numerous botanists have made significant contributions to the elucidation of the eastern Asian–eastern North American disjunct pattern of plant distribution during the twentieth century, both in the form of careful taxonomic studies of taxa exhibiting this distribution pattern and in summaries or overviews of current knowledge. Most of these contributions are well known to botanists and phytogeographers and many are included in our bibliography. However, much pertinent information is hidden in monographs, revisions, and other works under titles that often do not indicate a bearing on this topic.

The very useful summaries published by Hara (1952, 1956), Li (1952, reprinted 1971 with additions), Wood (1971, 1972), Raven (1972), and Thorne (1972), as well as papers published in this symposium volume, should be consulted for current views and numerous additional references not included here. Moreover, the volume edited by Graham (1972a) contains a collection of pertinent articles based on symposia held in conjunction with the XI International Botanical Congress in 1969 and a special Japan–United States Cooperative Science Program, which was also convened in 1969. While knowledge concerning the classic eastern Asian–eastern North America disjunct pattern of distribution has increased tremendously since the Linnaean era, much careful taxonomic work remains to be done before the relationships can be more fully understood and assessed. Darwin wrote to Gray in 1857 that "Undoubtedly careful discrimination of species is the foundation of all good work," and Wood (1972, p. 122) concluded his important paper by stating that "Morphology . . . is basic to the taxonomy of extant and extinct plants," and, consequently, to the study of disjunctions. It is perhaps appropriate to conclude this brief historical survey by reiterating these sentiments—our knowledge and understanding of the eastern North American–eastern Asian floristic connection will in large measure reflect and be determined by our knowledge of the systematics of the taxa involved.

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APPENDIX 1

Taxa indicated by Nuttall (1818) in his *Genera of North American Plants* as exhibiting disjunction between North America and Asia (occasionally also occurring disjunctly in other parts of the world). Comments by Pursh (1814) on the same genera are in brackets; "No" indicates that Pursh made no remarks. Our notes are in parentheses.

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7. **Leptandra virginica** (L.) Nuttall. "Common also to Japan, or more probably a distinct species of the same genus. A variety of this plant mentioned by Mr. Pursh, Vol. 1 p. 10, with purple flowers, may perhaps prove distinct. There is another species called *Veronica Sibirica,* inhabiting Dauria, in which the stamina and pistillum are double the length of the corolla." [No] (Now placed in *Veronicastrum* Fabricius.)

10–11. **Elytraria.** "Species. 1. *E. caroliniensis.* There are also 2 other species in India." [No]

80–81. **Manisurus** L. "A genus of India and America within the tropics, consisting of 2 species." [No] (One species is credited to North America by Nuttall.)

90. **Lechea.** "An American genus, with the exception of the *L. verticillata* of India." [No] (Five species credited to North America by Nuttall.)

92. **Cephalanthus** "Peculiar to North America; but scarcely differing from the *Nauclea* of India and Africa, excepting in the number of parts, which are 4 in place of 5." [No] (One species of *Cephalanthus, C. occidentalis,* recognized by Nuttall.)

94. **Oldenlandia.** "This genus appears to be almost equally divided between India and the tropical regions of America. The genus *Hedyotis* to which Mr. Elliott is inclined to refer the *O. glomerata* is also equally divided betwixt India and South America." [No]

98. **Cornus.** "Species . . . 8. *alba.* (The fruit of this species, though bitter and unpalatable, is eaten by the savages of the Missouri, from whence it seems to extend across the continent, and appears again in Siberia.) . . . Of this genus there are two other species in Europe, and 2 which are common to that continent, Asia, and America." [No]

127. **Polemonium.** "This genus appears as yet to contain but 2 genuine species; the other is common to Europe and Asia." [No]

152. **Claytonia.** "A North American genus, with the exception of *C. sibirica*; *C. lanceolata* of Pursh extends into Siberia, and *C. perfoliata,* which is annual, exists also in the island of Cuba within the tropic." ["I found a specimen collected by Pallas in the eastern parts of Siberia, perfectly agreeing with the present species." Pursh (p. 175) commenting on *C. lanceolata.*]

173. **Hydrolea.** "A genus of six species, (Sec. Persoon) indigenous to the tropical or warmer regions of America, with the exception of *H. Zeylanica* of India." [No]

174. **Heuchera.** "A North American genus, with the exception of *H. caulescens* discovered also in Kamschatka (sic) by the late professor Pallas." ["In the herbarium of A. B. Lambert, Esq. are specimens of a *Heuchera,* collected by Pallas in Kamtschatka, which appear to be the same with the present species." Pursh (p. 188), speaking of *Heuchera caulescens* Pursh.]

176. **Panax.** ". . . 2. *quinquefolium.* Gin-seng. Indigenous also to Tartary (sic)." (Nuttall's concept of *Panax* was much broader than it is today; he included several arborescent taxa, from New Zealand and the West Indies, and another herbaceous species, from New Holland, in the genus.) [No]

201–202. **Planera.** "Of this genus there is another species on the border of the Caspian sea." [No] (Now considered to be a monotypic genus of the southeastern United States.)

203. **Rhus.** "5. *Vernix.* also indigenous to Japan." [No]

205. **Aralia.** Speaking of the extra-North American taxa Nuttall said "The remaining species of this genus are indigenous to the tropical parts of America; there are also 3 species in Japan and 1 in China." [No]

212. **Mahonia.** "A third species of this genus is indicated by Mr. Pursh as indigenous to the kingdom of Nepaul (sic) in India; probably in a mountainous country." [Of *Berberis aquifolium* Pursh and *B. nervosa* Pursh, Pursh (p. 219) says: "The specific difference excluded, the description of the preceding species is applicable in every other respect, and together with another in the collection of A. B. Lambert, Esq., collected in Nepaul (sic) by Mr. Buchanon, forms a new division of the genus, with pinnated leaves; which probably may become a new genus, whenever the fruit is perfectly known, as the statement I have given of it was taken from a single and imperfect berry."] (The genus *Mahonia* was here described by Nuttall, *M. aquifolium* (Pursh) Nuttall, and *M. nervosa* (Pursh) Nuttall being the two American species recognized.)

223–224. **Erythronium.** "Of this genus there is but a single species out of America indigenous to Siberia and the south of Europe." [No] (Nuttall recognized three species in North America and suspected that a fourth, confused with *E. americana,* remained undescribed.)

224. **Uvularia.** "A North American genus with the exception of 2 species in Japan." [No] (Thunberg (1784) included three Japanese species in *Uvularia*; one of these is now treated as a *Tricyrtis,* another is a species of *Disporum,* the third is a *Fritillaria*; it is not known which two Japanese taxa were considered by Nuttall to belong to *Uvularia. Uvularia* is now considered to be endemic to eastern (mostly southeastern) North America.)

224–225. **Convallaria.** "1. *C. majalis.* Common also to Europe; flowers fragrant. There are but 2 other species of this genus as it is now constituted, indigenous to Japan." [No]

226–227. **Orontium.** "Of this genus there is a second species in Japan." [No] (Thunberg (1784) treated one species of *Orontium, O. japonicum* Thunberg; this is now placed in the genus *Rhodea* (Liliaceae), a genus with a peculiar aroid-like inflorescence.)

227. **Acorus.** "Common to Europe and North America, there is also a second species in China." [No]

239–240. **Trillium.** "A North American genus with the exception of *T. obovatum,* which grows also in Kamtschatka according to Pallas," ["*T. camtschaticum.* Pallas in herb. Lambert. In Canada near Montreal. . . . The specimens in the herbarium of A. B. Lambert, Esq., agree in every respect with those from Canada."] (Pursh (pp. 245–246) placed *T. camtschaticum* in synonymy under *T. obovatum.* Several species of *Trillium* are now known from Asia; no Asian and American species are conspecific.)

242. **Aesculus.** "A North American genus with the exception of *AE. Hippocastanum* of northern Asia." [No]

274–275. **Chimaphila.** (two species recognized, *C. umbellata* and *C. maculata*) "Indigenous also to the North West Coast of America.—Menzies. Probably both species of the genus will be found also in East Asia and Europe." [No]

284–285. **Hydrangea.** "An American genus, if we exclude *H. hortensis* of India, separated principally on the ground of its producing 3 styles, which is perhaps occasionally common to every *Hydrangea.*" [No]

285. **Tiarella.** "Species. 1. *cordifolia.* 2. *Menziesii.* 3. *trifoliata.* 4. *biternata.* A North American genus, of which Nos. 1 and 3, are also indigenous to Northern Asia." [No]

285–286. **Mitella.** "A North American genus with the exception of *M. nuda* of Northern Asia." [No] (Five species recognized by Nuttall.)

292. **Penthorum.** "According to Mr. Pursh there is a second species of the genus in China, collected by Sir G. Staunton." ["In the Herbarium of A. B. Lambert, Esq., is a second species brought by Sir George Staunton from China, which I distinguish by the following characters: *Penthorum Chinense,* caule simplici tereti, foliis elongato-lineari-lanceolatis subpetiolatis inaequaliter serratis, spicis cymosis terminalibus, seminibus ovatis corneis." Pursh, p. 323]

307. **Spirea.** "A genus almost equally divided betwixt Siberia and North America." [No] (Nuttall recognized 11 species in North America, one of which is now treated as *Aruncus dioicus* (Walter) (Fernald.)

309. **Dalibarda.** "2. *Fragarioides.* Flowers yellow. This species is also found in Siberia." (equals the currently accepted *Waldsteinia*) ["*Dryas trifoliata.* Pallas in Herb. Lambert." Pursh, p. 350]

309. **Geum.** ". . . 8. *radiatum.* 9. *peckii.* PH. Radical leaves reniform. Is this plant indeed a *Geum*? 10. *Anemonoides.* Also indigenous to Kamtschatka as well as No. 8. . . . A North American genus of which there are also 6 species in Europe, 1 in Japan, 1 in Barbary, 2 at the Straits of Magellan, and 2 equally indigenous to Kamtschatka and North America." (Pursh (p. 352) includes in the synonymy of *Geum radiatum* "*G. camtschaticum.* Pallas in Herb. Lambert." Of *G. anemonoides* Pursh says "On the north-west coast and the Kuril (sic) Islands.")

311–312. **Calycanthus.** "A North American genus with the exception of *C. praecox* of Japan." [No]

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10. **Actaea.** "Of this small genus there is 1 species indigenous to Europe and another to Japan." [No]

17–18. **Illicium.** "An American genus with the exception of *I. anisatum* of Japan and China." [No]

18. **Magnolia.** "A genus of about 15 species, almost exactly divided between China and the United States; there is also 1 species in tropical America." [No]

18–19. **Liriodendron.** "Of this genus there are 2 other species in China and 1 in the mountains of Amboina." (Amboina = island, Indonesia)

22–23. **Trollius.** "Of this genus there are 2 other species, 1 European and the other indigenous to Siberia." [No]

25. **Cyamus** (=Nelumbo) "Of this genus there is another species indigenous to the waters of India and Persia." (Nuttall considered two of the three species he listed for North America "*Pentapetalus*" and "*Reniformis,*" as being "doubtful.") [No]

35. **Dracocephalum.** "Principally a Siberian genus." [No] (Five species listed as being in North America by Nuttall.)

39. **Trichostema.** "Of this genus there is another species in Cochinchina." [No] (Three species treated for North America by Nuttall.)

44. **Bignonia.** (3) "This splendid genus of 60 or more species, is with a few exceptions in India, China, and Japan, exclusively indigenous to the tropical regions of America." [No]

98. **Oxytropis.** "A genus containing near 50 species, principally indigenous to Siberia, with the exception of a few species in Europe and the Levant." [No] (Nuttall recognized a single species in North America, and that from the north central United States.)

98–100. **Astragalus** L. "This vast genus of near 180 species exists principally in Siberia; there are a few species also in Europe and the Levant." [No] (Eleven species recognized for North America by Nuttall.)

107–108. **Lespedeza** Michaux. "A genus peculiar to

North America, there are, however, about 3 species indigenous to Siberia, of which *L. trichocarpa* ought to be compared with *L. capitata*; 3 other very doubtful species of India are added to this genus by Persoon." [No] (Eight species recognized in North America by Nuttall.)

118. **Robinia** L. "Excluding *Caragana*, the rest of this genus of 15 species is almost exclusively indigenous to tropical America, the only exceptions are 1 species in India and another in China." [No] (*Robinia* is now known to be a strictly New World genus; *R. pseudo-acacia* L., however, is widely naturalized in Asia and elsewhere.)

133. **Vernonia** Schreber. "An American genus with the exception of *V. anthelmintica* of India, the 10 other species comprising the genus are indigenous to the tropical regions of America." [No] (Seven species recognized for North America by Nuttall.)

159–162. **Solidago** L. "*Solidago* is exclusively a North American genus, with the exception of 5 or 6 species in Europe, and 2 near Canton in China. The arborescent species of St. Helena and New Zealand will probably be excluded from this genus, if ever carefully examined." [No] (Nuttall listed 51 species for North America.)

187. **Elephantopus** L. "A genus of 6 species indigenous to tropical America, with the exception of 1 in India." [No]

199. **Cypripedium** L. "Of this singular genus there are 3 other species in Siberia, 1 in Japan, and 1 in Europe." [No] (Six species listed for North America by Nuttall.)

219. **Liquidambar.** "1. *L. Styraciflua.* From New England to Florida, also indigenous to Mexico and extending to the shores of the Pacific Ocean. Of this genus there is a second species in the Levant." ["New England to Florida, and in all the western countries." Pursh, p. 635]

238–239. **Gleditschia** (sic) L. "Of this genus there appears to be another species indigenous to India and China." [No]

244. **Menispermum** L. "*M. canadense* is also found in Siberia." [No] (Nuttall recognized three species in the genus, all occurring in North America.)

CRETACEOUS AND CENOZOIC HISTORY OF THE NORTHERN CONTINENTS

WARREN HAMILTON[1]

The dispersal and migration of terrestrial plants and animals are controlled to a large extent by the distribution of land, sea, and orographic features and by climate. All these factors in turn are controlled in substantial part by the motions of the great plates that comprise the earth's outer shell, its lithosphere. Continents stand above sea level because of their thick, light crust, but they are parts of plates that also include the ocean floors. Seven very large plates, and numerous mid- and small-sized ones (the concept of coherent plates breaks down at the small-scale end), each typically 80 km or so thick, all move relative to all others. The plates tend to be internally rigid, and they interact mostly at their edges, although large, mostly continental parts of some plates undergo severe internal deformation. Velocities of relative motion between adjacent plates range upward to about 13 cm/year—an unimposing rate by human standards, but equivalent to enormous displacements when continued for tens of millions of years.

Spherical geometry requires that any motion between two parts of a spherical surface can be expressed as the rotation of one part relative to the other, defined by an angular displacement around an Euler pole of relative rotation. All trajectories of relative motions must be along small circles to that pole. (This pole is not to be thought of as having any mechanical significance.) The development of plate-tectonic concepts in the late 1960s was made possible by the demonstration that the relative motions that could be quantified fit these geometric requirements. The mechanisms causing plate motions are much debated, but the reality of the motions is proved.

Plates are now pulling apart primarily along the great submarine ridges in the world's oceans. As mantle wells up into the gaps between diverging plates at these spreading centers, part of it melts and is erupted on the surface as basaltic lava or is injected beneath the surface to crystallize as intrusive igneous rocks. The ridge stands high because its crust and mantle are hot, and hence are low in density. A steady state develops as the plates continue to move apart: the material at the ridge is hot when newly formed, but it cools and contracts as it migrates away, and the sea floor sinks to greater depths. The oceanic crust and upper mantle formed at spreading centers retain petrologic characteristics that can be recognized after subsequent events have brought them to other tectonic settings.

Where plates converge, one plate commonly tips down and slides beneath the other. Generally, an oceanic plate slides (subducts) beneath a continental plate (as along the west side of South America), or beneath another oceanic plate (as along the east side of the Mariana island arc). In either case, a magmatic arc—volcanoes at the surface, intrusive complexes at depth—tends to form in that part of the overriding plate that is about 100 km above the top of the subducting plate. Compositions of the magmatic rocks are quite different in continental and oceanic arcs. Sediments and other materials scraped off the top of the downgoing plate accumulate, snowplow fashion, in an accretionary wedge at the front of the overriding plate. Study of an accretionary wedge can reveal much about the character and history of oceanic lithosphere that has been subducted beneath the overriding plate.

Collisions result where light crustal masses are present on both of two converging plates, and any accretionary-wedge material is caught in the suture between the two. Collisions are often accompanied by severe internal deformation of one or both of such plates. Convergence commonly continues after a collision, but inasmuch as subduction of buoyant continental crust is difficult or impossible, subduction stops at the old site at which oceanic lithosphere had previously been subducted, and a new subduction system breaks through on the outer side of the continent as enlarged by the aggregation of the collided ma-

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terial. Actual collisions are commonly oblique rather than head-on, and they progress in one direction or another with time.

Strike-slip faults bound plates that slide past one another. Any strike-slip fault transfers spreading or convergence at one end to spreading or convergence at the other end. Many actual strike-slip boundaries are complex in detail and have obliquely convergent and divergent parts and also zones of distributed motion.

Plate motions are often illustrated by two-dimensional cartoons, many of which incorporate the false concept that the subducting plate is rolled over a platen fixed in the mantle and is injected down a fixed slot. All or most hinges actually migrate into the subducting plates as the overriding plates advance. Boundaries between adjacent plates tend to end at triple junctions, where three plates meet; such areas can display great variety and complex evolutions.

I have summarized the evidence for, and evolution of, these concepts elsewhere and have illustrated the development of a number of actual convergent-plate features (Hamilton, 1979).

Plate tectonics has operated throughout at least the last 2,500 million years—all of Proterozoic and Phanerozoic time. Continental rifting is recorded by truncations of basement terranes and by the deposition on the truncated margins of continental-shelf-and-slope stratal wedges. Subduction of oceanic lithosphere is recorded by most of the same structural and magmatic indicators that characterize modern tectonic systems; by aggregations through collisions of distinct continental masses and island arcs; and by paleomagnetic, paleoclimatic, and paleontologic indicators. The details of the processes, however, have changed with time. Thus, most of the earth's potassium had been cycled out of the mantle and into the continents before Paleozoic time; Phanerozoic granitic rocks are both voluminous and potassic only where their magmas have risen through Precambrian crust, or through voluminous sediments derived from such crust. Metamorphic rocks of blueschist facies, products of recrystallization at high pressures but relatively low temperatures within subduction systems, are voluminous in Mesozoic and Cenozoic terranes, progressively less common in older Paleozoic ones, rare in late Proterozoic terranes, and unknown in older tracts; the earth probably is cooling and losing heat at a progressively decreasing rate. Surface temperatures, however, are determined primarily by the sun, and they have not varied widely within the last 3,800 million years—the age of the oldest rocks known—for liquid water has always been present, and continental glaciation has occurred intermittently during the last 2,000 million years at least.

During Archean time, 2,500 to 3,800 million years ago (Ma), continents were formed by magmatism more intense than that of later time, in ways that are much disputed, but that many of us regard as the result of rapid motions of small lithosphere plates. Even then, however, the earth must have lost heat primarily through spreading oceans and by subduction-related magmatism, because the crustal geothermal gradients recorded by petrologic indicators in deeply eroded Archean rocks are much like those in young terranes. Before 3,800 Ma, whatever crust the earth possessed was so thin, and destructive (remelting?) processes were so effective, that no rocks then formed have been recognized.

No beginning in time can be seen for plate motions. The earth's lithosphere has always consisted of rifting, drifting, subducting, and colliding plates. All continents are aggregates of fragments, sutured together at times past. Continents have been deformed complexly by strike-slip faulting and by oblique and orthogonal rifting and compression, and the process continues. Reconstructions of prior positions of land masses become progressively more ambiguous as the age considered increases. Although valiant attempts have been made at reconstructions for all of Phanerozoic time (e.g., Smith et al., 1981, and Ziegler et al., 1979) and even for the late Precambrian, such reconstructions ignore most pre-Jurassic sutures and continental deformation, are constrained primarily by approximate latitudes inferred for some of the bits, and are schematic at best. Even for Cretaceous time, major uncertainties exist regarding the geometry of eastern Siberia and Alaska; of the entire Tethyan region (Central America, Caribbean, Mediteranean, Alpine Europe, North Africa, middle East, Himalayas, Southeast Asia, Indonesia, Melanesia); of onshore and offshore East Asia; and of the Scotia-West Antarctica region. Many of the ambiguities are more likely to be resolved by paleobiogeographic studies than by geologic and geophysical ones.

The biogeographic consequences of plate motions and interactions must be enormous. For example, a small landmass on a moving plate

can carry a terrestrial biota derived partly from a biota shared with some previously adjacent landmass, and derived partly by fortuitous immigration, both components evolving more or less in isolation as the landmass moves with time through different climatic zones. The configuration and surface altitude and, hence, the amount and distribution of land above sea level, can change radically with time. When two landmasses collide, their biotas mingle and compete. Pre-collision fossil biotas of the two lands are different, whereas post-collision biotas are shared.

This paper briefly summarizes some tectonic factors that may be relevant to the biotic relationships of the northern continents during Cretaceous and Cenozoic time. Little mention is made of the biotic features themselves.

North American and Eurasian Plates

North America north of Mexico, and Eurasia north of the Alpine-Himalayan mountain system, behaved as internally coherent continental plates during Cretaceous and Cenozoic time, although they had complex histories of pre-Cretaceous sundering and aggregation, and although they were much deformed internally during the Cretaceous and Cenozoic. The two megaplates began to separate in middle Cretaceous time, and the Atlantic Ocean has been widening ever since. Relationships between Siberia and North America throughout this time are poorly understood. The following presentation is concerned with some internal and marginal features of the two megaplates, and not with relationships between the megaplates.

North American Plate

Tectonic accretion of western North America. Much of the western part of the North American Cordillera consists of material added to the continent by subduction processes during Jurassic and Cretaceous time, and to a lesser extend during Cenozoic time. Alaska (e.g., Jones & Silberling, 1979), southwest Yukon Territory and the southwestern two-thirds of British Columbia (e.g., Tipper et al., 1981), and most of Washington, Oregon, and western California (e.g., Hamilton, 1978) consist largely of continental fragments, island arcs, and assorted debris scraped off oceanic lithosphere plates, and of magmatic rocks formed in response to subduction and to rifting. Paleontologic and paleomagnetic evidence requires that some of these materials were conveyor-belted many thousands of kilometers to their present North American sites. The aggregate width of the accreted materials generally increases northwestward along the continental margin, from 50 to 100 km (much of that offshore) in Baja California and southern California, through 500 km in Washington and Canada, to 1,000 km in Alaska. Throughout Cretaceous and Cenozoic time, the oceanic and continental-margin materials have had northward components of motion relative to interior North America, whether the specific motion has recorded oblique subduction, oblique extension, or strike-slip.

All the fragments of continental materials presumably carried significant biotas if they stood above the sea before collision, but none is known to have been other than a briefly detached bit of North America. Conversely, the fragments for which distant origins are likely are largely of submarine origin, although some may have included small islands before collision. I know of no biotic interchanges that can be ascribed to the accretion of any of the fragments, although juxtaposed fossil assemblages are grossly disjunct in many places.

Western Interior seaway. The Western Interior of the United States and Canada—a region that is now at generally high surface altitude in such provinces as the High Plains, Colorado Plateau, and much of the U.S. Rocky Mountains—was inundated by a shallow sea that connected the Gulf of Mexico and the Beaufort Sea during middle Cretaceous time (McGookey et al., 1972; Rudkin, 1966; Williams & Burk, 1966). Seas transgressing south from the Arctic and north from the Gulf of Mexico joined in late Albian (latest Early Cretaceous) time, and the seaway remained more or less continuous until about early Campanian (middle Late Cretaceous) time. There was then widespread regression of the sea in Canada, but the Western Interior of the United States remained broadly inundated through most of the rest of Late Cretaceous time. The middle Cretaceous seaway was continuous between the Gulf of Mexico and the Canada Basin of the Arctic Ocean and must have much hindered east-west migration of terrestrial organisms. Cenozoic marine flooding of the continental margins was relatively minor.

Central America-Gulf of Mexico-Caribbean Sea. From the end of Triassic time until late in Pliocene time, North and South America were separated by water, although tectonic and vol-

canic lands may have connected them at times, and although continuity may have been maintained via Europe and Africa during much of Mesozoic time. The shapes and positions of landmasses within Mexico, Central America, and the Caribbean have changed greatly with time and are still only partly understood (Pindell & Dewey, 1982). Although subduction complexes have joined the continents at times, submarine gaps largely blocked migration of land organisms during Cretaceous and Tertiary time. The great intercontinental biotic interchange began only about three million years ago, when the Isthmus of Panama rose above sea level (Keigwin, 1978).

Internal deformation of North America. Alaska, western Canada, and the western United States were much deformed by lateral motions during Cretaceous and Cenozoic time. In addition to marginal tectonic accretion, an array of compressional, extensional, rotational, and strike-slip deformation (e.g., Hamilton, 1978) caused complex changes in orographic configurations, and hence much influenced climates, but did not produce any major seaway that would have impeded biotic interchanges.

Deformation in Eastern Canada, Greenland, and Alaska, is discussed in subsequent sections.

EURASIAN PLATE

Tectonic accretion of southern and eastern Eurasia. Eurasia is a composite megacontinent formed throughout Phanerozoic time by the aggregation of large and small subcontinents and of varied oceanic debris swept up between them, as intervening oceanic lithosphere was subducted (e.g., Burrett, 1974, and Hamilton, 1970). Northern sutures are in general older than southern ones. The land masses south of the Alps, Carpathians, Lesser Caucasus, and Himalayas have collided with Eurasia during Late Cretaceous and Cenozoic time (e.g., Burchfiel, 1980; Dewey et al., 1973; Sinha Roy, 1978). The accretion is still going on in both the west, where Africa and Arabia are in the process of closing with the northern continent, and in the east, where Australia has been colliding with island arcs migrating away from Asia (Hamilton, 1979). Continental masses have converged as intervening oceanic crust sank beneath one or both of them. Bits of continents have rifted, rotated, and re-aggregated. Island arcs have migrated, and changed their configurations, between converging continents. Shapes of colliding masses changed as they were crushed together.

Each of the arriving continental plates must have carried with it immigrant plants and animals and an assemblage of fossils—both different from those of the newly adjacent mainland. Thus, the middle Tertiary contact between Africa and Eurasia allowed horses to walk onto Africa and elephants onto Eurasia. Smaller islands must have carried limited biotas, evolved in varying isolation. Biotas were derived partly from the continent from which they rifted away; other biotas were derived partly from overwater immigrants. Thus, the middle Tertiary collision of Australia with island arcs that migrated from the margin of Asia caused much of the limited exchange of attenuated and variably evolved biotas between those two continents (Hamilton, 1979).

Seaways between Europe and Asia. During much of Late Jurassic and Early Cretaceous time and part of the early Tertiary, central Eurasia was covered by broad shallow seas that extended from the Tethyan ocean on the south to what is now the Arctic Ocean on the north (Grossheim & Khain, 1967; Vereshchagin & Ronov, 1968). During Late Jurassic and most of Early Cretaceous time, a seaway west of the Urals connected what are now the Caspian and Barents Sea regions. By late Early Cretaceous time (Albian, possibly also Aptian), the sea had receded from the northern part of this region, and dry land has connected the Russian Platform and the Urals ever since. East of the Urals, another broad, shallow sea transgressed southward during early Late Cretaceous (Cenomanian) time and covered what are now the West Siberian Lowlands through most of remaining Cretaceous, Paleocene, and Eocene time. Shallow seas also covered much of the Caspian-Aral region to the south, but between about 50° and 54° present latitude, northern and southern areas were separated by land, except that a more or less continuous seaway connected between northern and southern seas during most of Eocene time. Both eastern Russia and the West Siberian Lowlands were emergent in Oligocene and later time.

During much of the Early Cretaceous and again during most of the Eocene, marine water thus separated northern Europe and Siberia within what is now the USSR, although the sea may have regressed enough intermittently to provide land corridors between east and west. The Eocene seaway connected flooded continental shelves, beyond which were deep oceans, to the north and south, so migration of land biotas would have been severely hindered. The Early Creta-

ceous seaway similarly extended to deep ocean in the south and probably did so in the north also.

Internal deformation of Eurasia. South of about latitude 45° in Europe and 55° in Asia, Eurasia has been deformed by Cretaceous and Cenozoic extension, compression, and strike-slip motions, in addition to the accretion of land masses to the south and east margins of the continent (e.g., Alvarez et al., 1974; Burchfiel, 1980; Cohen, 1980; Dewey et al., 1973; Dewey & Sengor, 1979; Hamilton, 1979; Molnar & Tapponnier, 1975; Tapponnier & Molnar, 1979). Distribution and character of mountains, plateaus, basins, and deserts has changed complexly, but the general continuity of land in the main part of the continent, independent of accretion and rifting effects and the seaway just noted, has not.

OPENING OF THE ATLANTIC OCEAN

At about the end of Triassic time, North and South America, Africa, and western Europe were parts of a single large continent, the product of the suturing together of various lesser continents during Paleozoic time. Eastern Europe and Asia were bounded on the south by the broad Tethyan ocean. India and various lesser continental pieces of alpine Europe and the Middle East were not yet in contact with the northern continent. The subsequent opening of the North Atlantic is reasonably well constrained by the fitting together of ocean-floor magnetic anomalies (which are products of sea-floor spreading dated by deep-ocean drilling) and of the margins of continental crustal masses (Fig. 1). Following and accompanying tensional thinning of the continents along what became the Atlantic, North America plus Europe began to move northwestward away from Africa plus South America, in Middle Jurassic time, about 165 m.y.a. Europe and North America remained attached to one another; Iberia, at the southwest corner of the European plate, slid past Africa when the Atlantic opened beween the eastern United States and northwest Africa (Sclater et al., 1977). Simultaneously, the Gulf of Mexico, plus oceanic lithosphere since overridden by the eastward-expanding Caribbean plate, opened between the southern United States and South America. These motions continued until the end of Early Cretaceous time, about 95 Ma. The configuration of Central America and the Caribbean region during this time, and indeed during Late Cretaceous and early Tertiary time, is poorly constrained; continuous old continental lithosphere did not connect North and South America, but tectonic or volcanic lands may have joined them at times. Dry-land connections between the Americas, however, might have been maintained, at least intermittently, during Jurassic and Early Cretaceous time via Africa, Iberia, and western Europe.

The motion pattern changed greatly at about the beginning of Late Cretaceous time, and the Atlantic Ocean began to open; North and South America have been moving mostly westward since then, with little relative motion between them, away from Africa plus Europe. Sea-floor spreading was simple in the South Atlantic, and in the North Atlantic as far north as Newfoundland and Britain: the ocean widened steadily at the center, although at varying rates (Sclater et al., 1977).

PLATE BOUNDARIES BETWEEN THE ARCTIC AND ATLANTIC OCEANS

North of the latitude of Ireland, the spreading history of the Atlantic Ocean has been complex, patterns have changed with time, and transform faults have stepped spreading into the Arctic. Between the start of spreading in the middle Cretaceous and about 60 Ma in the Paleocene, spreading was concentrated west of Greenland, in the Labrador Basin; from about 60 to 38 Ma, spreading occurred both east and west of Greenland, although that to the west was very slow after about 50 Ma; since 38 Ma, spreading has taken place only east of Greenland (Jackson et al., 1979; Kristoffersen & Talwani, 1977; Sclater et al., 1977; Eldholm & Talwani, 1977; Vogt, Perry et al., 1981). Spreading between Norway and Greenland has jumped from rift to rift, and has not been confined to a single medial rift continuous in time.

ARCTIC ATLANTIC

The Arctic sector of the Atlantic Ocean—the Greenland and Norwegian Seas—opened as Greenland moved away from Norway. This spreading system ends at transform faults, along and southwest of the submerged continental margin of Spitsbergen and the Barents Shelf. These faults step the spreading into the Eurasian Basin of the Arctic Ocean, within which the spreading axis trends to the Siberian continental margin near the delta of the Lena River.

Until about 38 Ma, Spitsbergen and north-

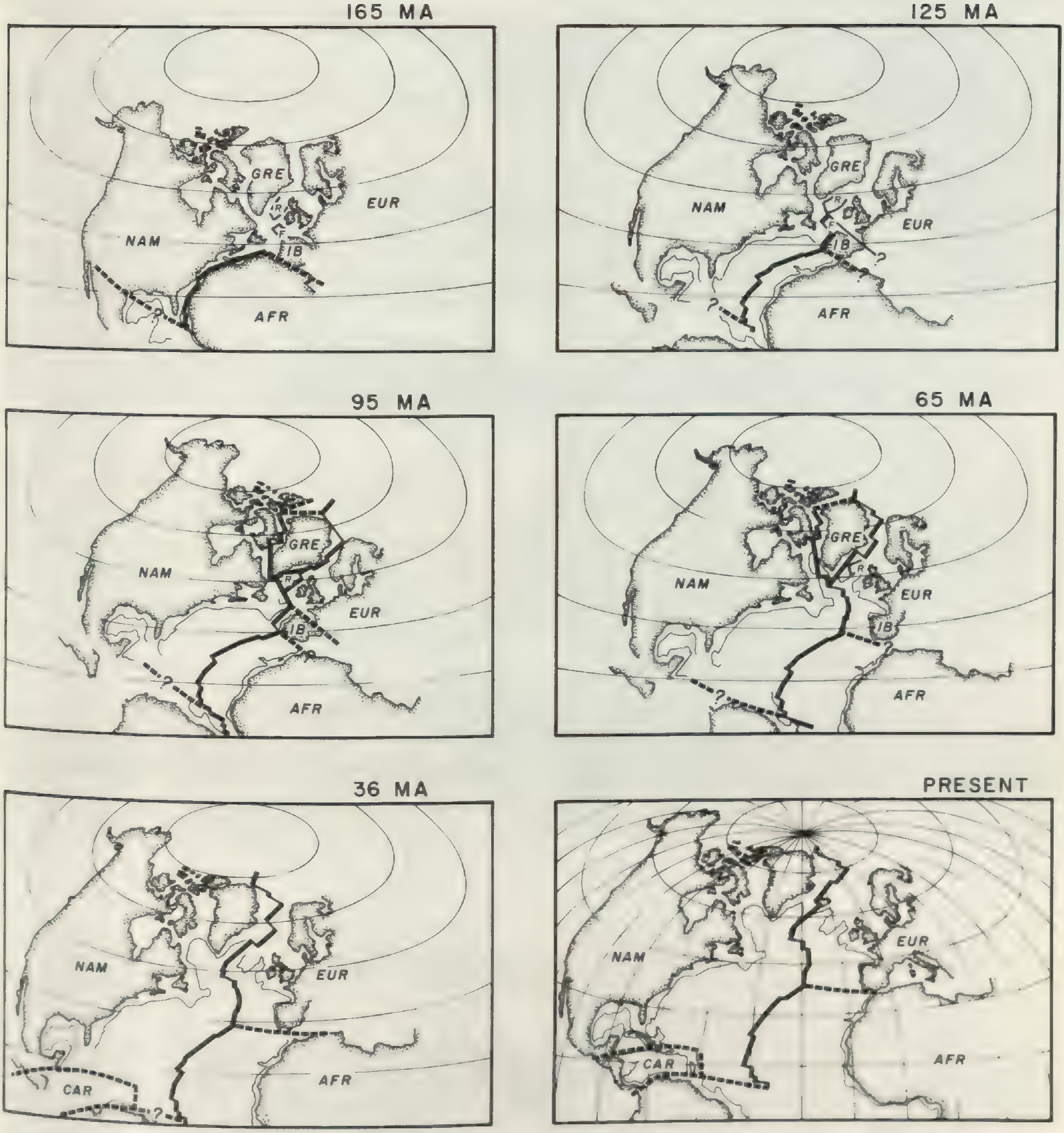

FIGURE 1. Tectonic history of the North Atlantic Ocean, showing positions of continental masses from Middle Jurassic time (165 Ma) through Early and middle Cretaceous (125 and 95 Ma), Cretaceous-Tertiary boundary time (65 Ma), and early Oligocene (36 Ma). NAM, GRE, EUR, CAR, IB, AFR, F, and R represent respectively North America, Greenland, Eurasia, Caribbean, Iberia, Africa, Flemish Cap plus Orphan Knoll, and Rockall Bank. The 2,000 m bathymetric contour around each continent is shown with a light line; heavy lines represent active spreading centers; dashed lines represent plate boundaries of unspecified types. Reproduced, with permission, from Sclater, Hellinger and Tapscott (1977, fig. 3), Journal of Geology, v. 85, p. 517, copyright by University of Chicago.

east Greenland were sliding past one another on a transform fault trending north-northwestward, and continental crust was continuous between them (Talwani & Eldholm, 1977; Vogt, Bernero et al., 1981, fig. 2). That this slip had a small compressive component is shown by the Paleogene deformation of southwest Spitsbergen. At about 38 Ma, the slow spreading between Greenland and North America ceased, the motion of Greenland became northwestward relative to Norway, and oblique extension began between Greenland and Spitsbergen; the result was

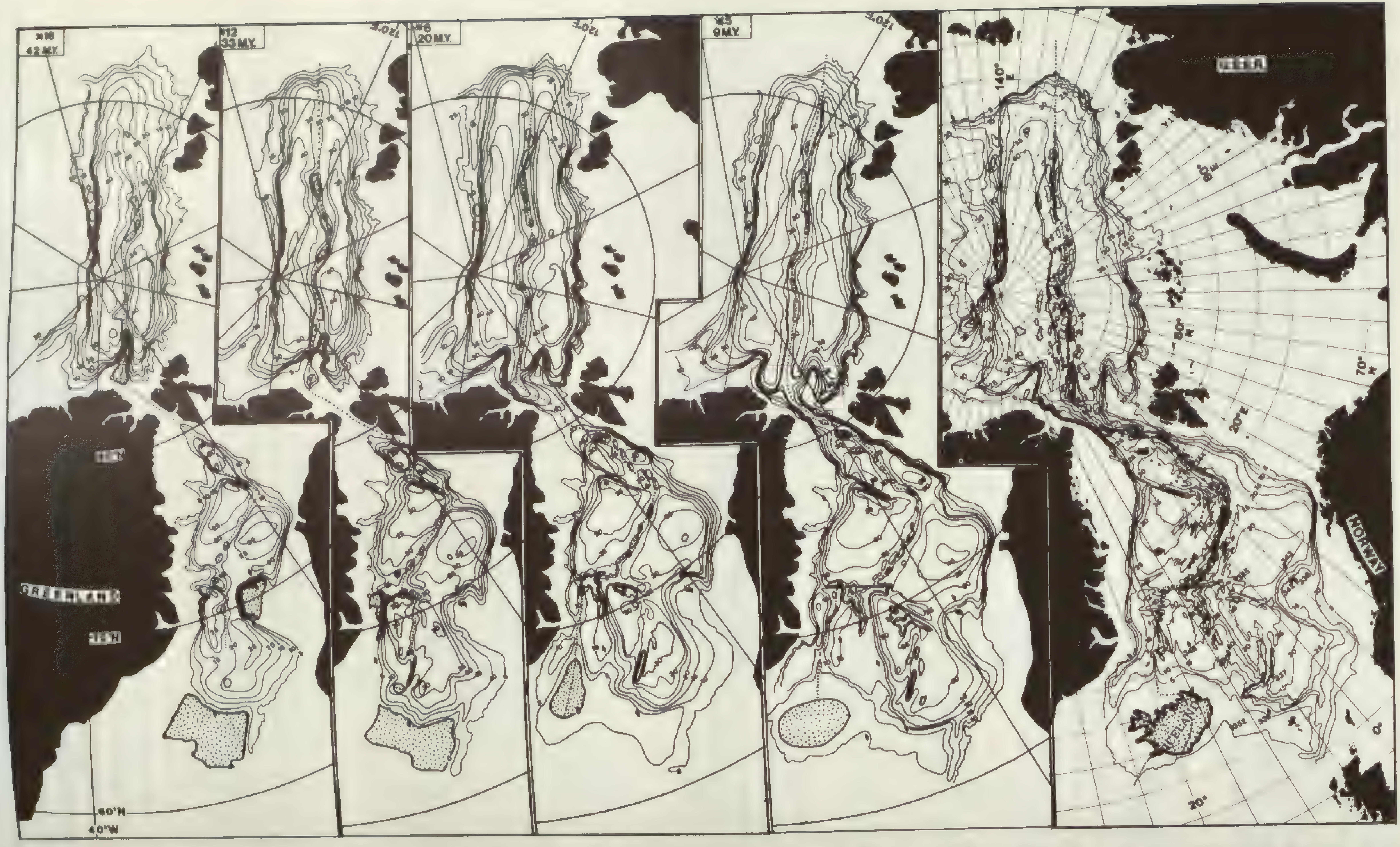

FIGURE 2. Present bathymetry of the Greenland-Norwegian Sea and the Eurasian Basin of the Arctic Ocean (right), and paleobathymetry in late Eocene, middle Oligocene, and early and late Miocene times. Contour interval 500 m, labeled in 100s of meters. Derived by matching magnetic anomalies of the indicated numbers and ages, and integrating with known age/depth curves for subsidence of oceanic lithosphere. Reproduced, with permission, from Vogt, Bernero, Kovacs and Taylor (1981, fig. 5).

a shallow seaway on thinned continental crust between them, followed by a narrow but deep and widening oceanic rift from about 30 Ma (Talwani & Eldholm, 1977; Vogt, Bernero et al., 1981).

Land connections. Dry land thus could have connected Greenland and Spitsbergen throughout Cretaceous and early Paleocene time (before most spreading occurred in the Arctic Atlantic) and during much or all of the rest of Paleocene and Eocene time (while continent-against-continent transform faulting was underway). Further, great basalt plateaus were built during Tertiary time on oceanic crust between Scotland and East Greenland, and these might have provided an intermittent land bridge before some time in the Miocene (Eldholm & Thiede, 1980).

Spitsbergen is now separated from Norway by the shallow sea of the continental Barents Shelf. Seismic-reflection data indicate that the strata beneath this shelf are mostly of pre-Cenozoic age (Eldholm & Talwani, 1977), so the shelf may have been emergent during much of Cenozoic time.

BAFFIN BAY AND LABRADOR SEA

The early, western center of North Atlantic spreading between Labrador and Greenland is represented by the oceanic Labrador [Sea] and Baffin [Bay] Basins. Magnetic anomalies, drilling data, and seismic-reflection surveys indicate that new ocean floor was forming in the Labrador Basin between Greenland and Labrador by a little before 75 Ma, earlier Late Jurassic and Cretaceous motion having been accommodated by extensional thinning of the continental margins (Hinz et al., 1979; Johnson et al., 1982; Le Pichon et al., 1979; Srivastava, 1978). Southern Greenland moved relatively northeastward away from Labrador until about 60 Ma; then, the relative motion slowed and changed to about north-northeastward, and spreading accelerated between Norway and Greenland. Motion between Greenland and Labrador ceased about 38 Ma.

The history of the northern part of the rift, between Greenland and Baffin Island, is less well known. Baffin Basin is floored by oceanic crust; magnetic anomalies trending north-northwestward indicate sea-floor-spreading of possible Paleocene and Eocene age in the deep, central part of the basin (Jackson et al., 1979; Keen et al., 1974). A Late Cretaceous age can be extrapolated for the margins of the oceanic rift, and for extensional thinning and faulting of the continental shelves prior to complete rifting. Upper Cretaceous marine strata are present on the Baffin Island continental shelf (MacLean & Falconer, 1979).

If the Baffin Basin anomalies are identified correctly as of Paleogene age, then the width of Paleogene ocean formed between Greenland and North America changes little within the Labrador and Baffin Basins; the Euler pole of relative rotation is distant, and northeast-trending transform faults step spreading from one basin to the other through the Davis Strait region.

Reconstructions between Greenland and Canada are complicated by crustal extension and basaltic magmatism along the margins of Baffin Bay and the Labrador Sea. Continental margins are thinned by extension accompanying rifting, and wedges of strata that prograde across them maintain continental shelves. Something like half the width of the shelf and continental slope shallower than 2,000 m along a rifted continental margin may typically represent extension of continental crust. The uncertainties of such extension are quantitatively most important for reconstructions of narrow ocean basins, such as those of Baffin Bay and the Labrador Sea. These uncertainties are further complicated by new crust built of very thick lower Tertiary basalts of mantle origin, onshore and offshore of west-central Greenland between 68° and 73°N, and on easternmost Baffin Island and the shelf east of southeastern Baffin Island (Keen et al., 1974; see also Johnson et al., 1982). Davis Strait, between the Baffin and Labrador Basins, is only 500 to 1,000 m deep and has crustal characteristics of a basalt plateau (Keen et al., 1974).

The Late Cretaceous magnetic anomalies of the Labrador Basin indicate an Euler pole of relative rotation between Greenland and North America somewhere near Alaska, and from this it can be predicted that the amount of Cretaceous spreading should decrease northwestward through Baffin Bay. This prediction is not fulfilled: southeastern Baffin Bay is too narrow, even if much of the width of its flanking continental shelves be assumed to represent spreading. Other plate boundaries northwest of the Labrador Basin must accommodate some of the Cretaceous spreading. The problem is alleviated but not eliminated if the central Baffin Bay magnetic anomalies are partly of Cretaceous age. Interpretations developed here are illustrated by Figures 3 and 4.

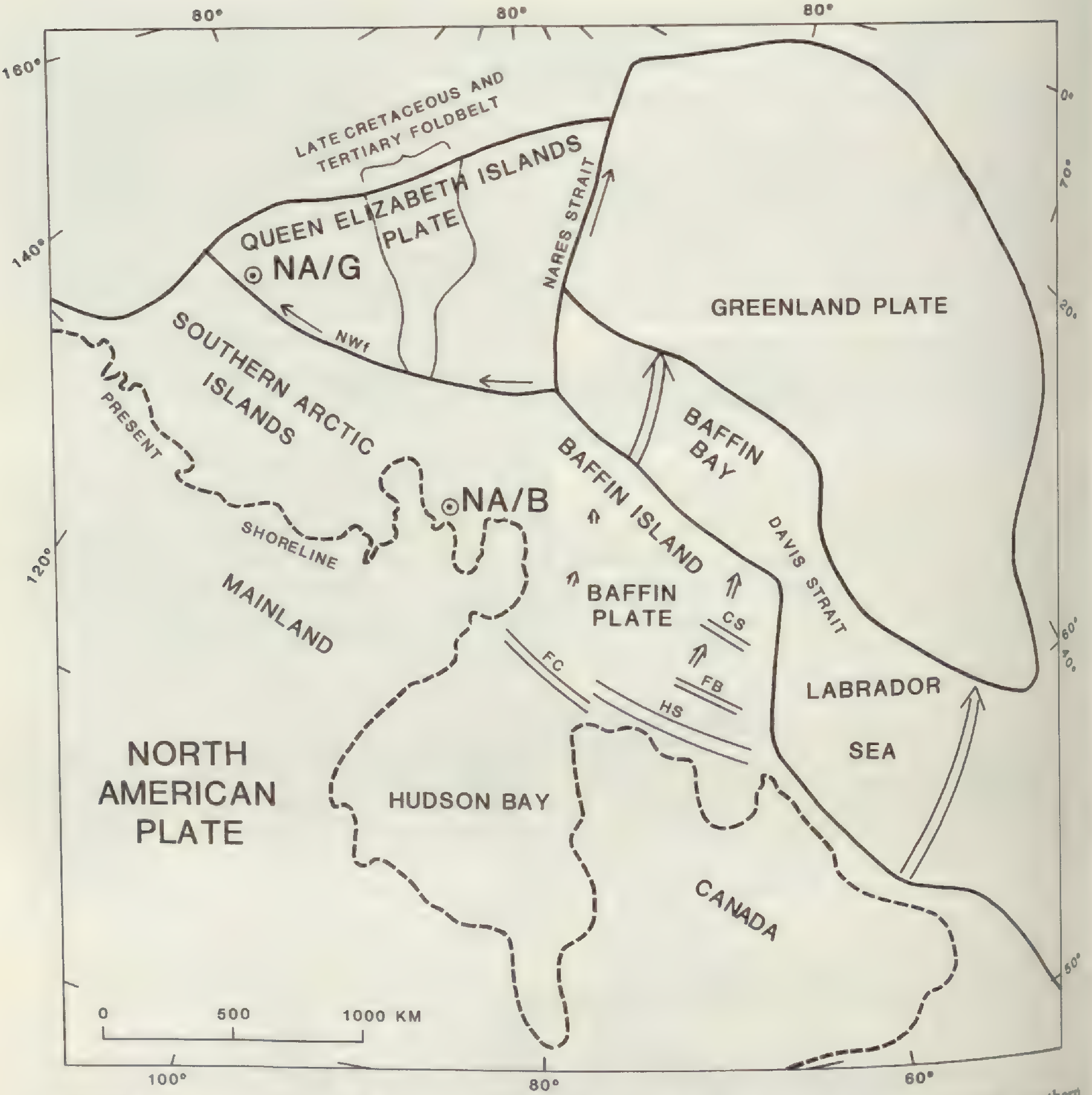

FIGURE 3. Schematic illustration of Cretaceous and Cenozoic plate motions inferred within the northern Canada-Greenland region; Atlantic and Arctic Ocean features are not included. Double arrows show overall motions relative to mainland Canada; single arrows show motions across strike-slip (transform) faults. Euler poles of relative rotation of plates shown by circles: NA/G, Greenland and mainland Canada; NA/B, Baffin Island and mainland Canada. Other abbrevations: CS, Cumberland Sound graben; FB, Frobisher Bay graben; FC, Fox Channel graben; HS, Hudson Strait graben; NWf, Northwest Passage fault. Reconstruction using these boundaries requires counterclockwise rotation of Nares Strait fault relative to Northwest Passage fault; the Tertiary foldbelt of the northern Arctic Islands is assumed to be the product of the resultant compression. Only the mainland Canadian shoreline is shown.

ROTATION OF BAFFIN ISLAND

Rotation of an internally fragmented Baffin Island lithosphere plate, counterclockwise relative to both Greenland and mainland North America, provides the likely explanation for much of the problematic geometry. Although Baffin Island generally has been assumed to be part of the rigid North American plate, its internal and marginal geology indicate otherwise (as Rice & Shade, 1982, recognized). Mainland Canada plus shallow Hudson Bay are separated from Baffin Island plus shallow Foxe Basin by the southeast-widening graben systems of Foxe Strait and Hudson Strait. These grabens contain Paleozoic strata

in a region otherwise surfaced now mostly by Precambrian basement rocks (Sanford, 1974). Similar grabens containing Paleozoic strata form Frobisher Bay and Cumberland Bay, in eastern Baffin Island (MacLean & Falconer, 1979); young normal faults cross southern Baffin Island at least along the Frobisher Bay trend. Normal faulting requires crustal extension. The amount of faulting, and hence probably also of extension, decreases northwestward, so Baffin Island apparently has rotated counterclockwise relative to mainland Canada.

The Euler pole of that relative rotation might lie along the boundary between the Baffin and Canadian plates, in which case crustal compression should exist beween the plates along their boundary to the north of that pole, or the Euler pole might lie beyond the north limit of the boundary (here taken to be the Northwest Passage fault), in which case the boundary should be entirely extensional. Published geologic data appear to permit either interpretation. Cambrian to lower Tertiary strata are broken by numerous faults and monoclines, mostly trending northwestward, in northern Baffin Island and adjacent areas. Although the faults have been termed normal by all geologists who have mapped them, the strata of the downdropped sides rise toward some of the faults in moderately-dipping monoclines. Thus, the Eclipse trough, which contains 3 km of exposed middle Cretaceous to lower Eocene fill, and probably contains more beneath its submarine portion, has a marginal monocline, with basinward dips of as much as 40°, along its faulted northeast boundary (Jackson & Davidson, 1975; Miall et al., 1980). This geometry, and the presence of open folds away from faults, permit the inference that the Cenozoic deformation is compressional, rather than extensional, in this northern region. (I have seen no statements regarding actual observations of dips of Cenozoic faults.) Further, some of the compressive deformation of the Boothia uplift, west of northern Baffin Island, is possibly of Cretaceous or early Cenozoic age. The straightness and continuity of some of the Phanerozoic faults (e.g., Blackadar et al., 1968) of west-central Baffin Island, however, permit an inference of dominantly strike-slip faulting there.

Cretaceous and Paleogene extension on the order of 100 km might reasonably have produced the normal faulting in the southeast Baffin region. (Rice & Shade, 1982, suggested 80 km.) An Euler pole in the region of 69°N, 86°W, near Melville

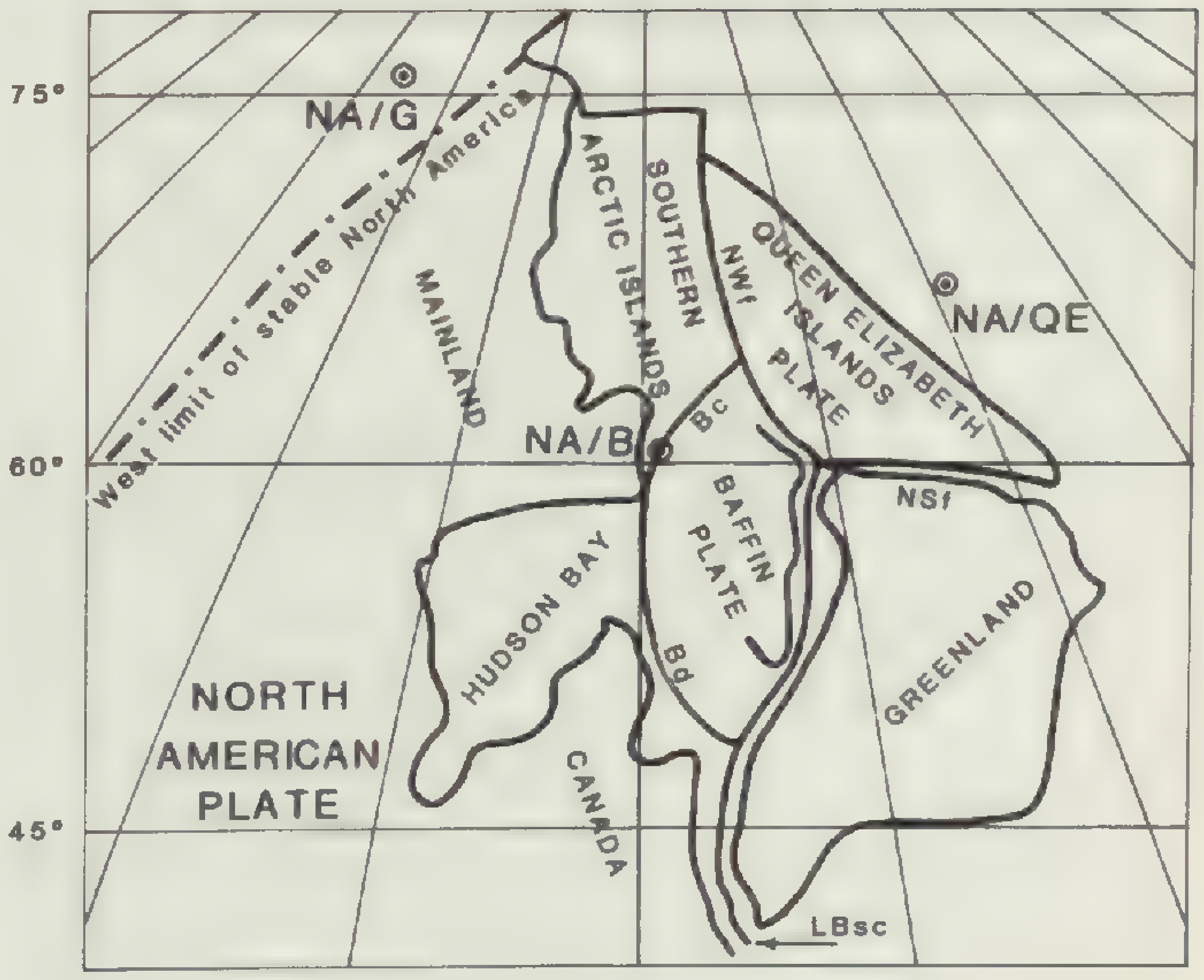

FIGURE 4. Reconstruction of Greenland and northeast Canada in middle Cretaceous time. Present shorelines of mainland Canada, northeastern Baffin Island, and Greenland are shown; boundaries of Arctic-island groups are generalized. The paleolatitudes correspond to a North American paleomagnetic pole position of 68°N, 173°W, after the compilation by Van der Voo (1981). Longitude lines are 15° apart and illustrate the equal-area projection. Plate boundaries marked by heavy lines: LBsc, Labrador Basin-Baffin Basin spreading center; NWf, Northwest Passage transform fault; NSf, Nares Strait transform fault; Bc and Bd, convergent and divergent parts, respectively, of boundary between Baffin Island and North American plates. Circles show Euler poles of subsequent relative rotations of plates: NA/G, North America and Greenland; NA/B, North America and Baffin Island plate; NA/QE, North America and Queen Elizabeth Islands plate. Arctic and Atlantic Ocean features, and Eurasian, Alaskan, and Cordilleran landmasses, are not depicted.

Peninsula, would account for the normal faulting of the southeastern Baffin region by orthogonal extension; for strike-slip faulting in west-central Baffin Island; and for crustal shortening in northern Baffin Island and any young component of shortening in the Boothia uplift—*if* these disparate elements are all of the same age and are characterized correctly in this scenario. Adoption of such an Euler pole, plus the assumption of 100 km of extension in the southeast, would predict about 5° of rotation, and hence about 70 km of total crustal shortening between northeast Baffin Island and the mainland west of the Boothia uplift. If, however, the Boothia compression is entirely older, and the north Baffin structures are extensional rather than compressional, then the Euler pole lies farther northwest, beyond the Northwest Passage. Such a pole would require a smaller angular rotation of the Baffin plate. Either interpretation can be inte-

grated with the motions defined for the opening of the Labrador Basin to account for the observed progressive northwestward decrease in the net motion between Baffin Island and Greenland.

SEAWAY

The history of rifting, oceanic circulation, and paleoclimates was deduced by Gradstein and Srivastava (1980) by study of microfossils from wells on the shelves flanking the Labrador Basin, and from two deep-water wells in the basin. A seaway west of Greenland probably connected the Atlantic and Arctic Oceans most of the time from the late Late Cretaceous (Maestrichtian) on. The Northwest Passage may have been the main early channelway between Baffin Bay and the Arctic Ocean. In the Maestrichtian, and again in the early and early middle Eocene, subtropical Gulf Stream waters reached about as far north as present latitude 50°N (paleolatitude about 35° or 38°); water was cooler during the Paleocene and again during the middle Tertiary, but there probably was a general northward flow of water toward a nonglacial Arctic Ocean. By late Miocene time, the cold, south-flowing Labrador Current was in existence and glacial conditions presumably existed in the Arctic.

TRIPLE JUNCTION AT THE NORTH END OF BAFFIN BAY

The 450 km or so of spreading of northern Baffin Bay represents plate motions that could not have stopped at the north end of the bay, and that must have been accommodated on other plate boundaries to the north of Baffin Island and Greenland. The various proposals for these boundaries in the literature include a ridge-transform junction, a ridge-ridge-ridge triple junction, a ridge-trench junction, a pivot between spreading and compression, and rejection of plate tectonic concepts. None of these proposals fits both the geometric requirements and the known geologic and geophysical parameters, and I do not discuss them here. Instead, I note evidence of a triple junction between the Baffin Bay spreading center and two left-slip transform faults. One of these faults follows narrow Nares Strait north-northeastward from the north end of Baffin Bay, separating Greenland and Ellesmere Island. The other fault trends westward from the north end of Baffin Bay, along the aligned straits of the Northwest Passage. Fault, fault, and spreading center meet at mutual angles of about 120°. Neither fault is itself in a transform (small-circle) relationship to any likely spreading direction between Greenland and Canada; but by postulating simultaneous motion on both faults, the separation of Greenland from mainland Canada can be reconciled with Arctic geology.

Nares Strait fault. The linear trend of Nares Strait north-northeast from the head of Baffin Bay, between Ellesmere Island and Greenland, continues beyond Ellesmere as the north edge of the submerged continental margin of North Greenland (Figs. 3 and 5). The strait was assumed by Wegener (1920), and by most subsequent investigators of continental drift and, later, of plate tectonics, to mark a strike-slip fault having about 250 km of left slip, related to the opening of Baffin Bay.

I believe that such a fault does indeed exist. Many geologists disagree. A symposium on evidence for and against the fault was convened in 1980, and its results were published in a volume edited by Dawes and Kerr (1982). In general, symposium authors concerned with plate reconstructions showed that no geometric alternative to a strike-slip fault has been recognized, whereas most of the geologists familiar with the geology on one side or the other of the strait argued for little or no faulting. The latter group collectively presented an impressive number of arguments against major faulting by projecting geologic zones and lines across the strait with little or no offset, as summarized by Dawes and Kerr in the final paper in the book. Having examined the primary geologic literature on both sides of the strait—reconnaissance 1:250,000 geologic maps and various reports and monographs for Ellesmere, more limited materials for Greenland—I regard none of the anti-fault arguments as proved and, hence, regard their sum also as unconvincing.

The critical components at issue are lines representing changes in sedimentary facies and style of deformation in Paleozoic strata on both sides of the strait. Some such lines are drawn without offset across the strait by the anti-fault geologists but are unconstrained on one side or the other, and hence are irrelevant. Others could be constrained by data on both sides but instead appear to be drawn schematically where they might cross the strait, if indeed there were no faulting, not where the data placed them independently. On the contrary, the front of deformation in Paleozoic strata, the hinge line between platform and continental shelf Paleozoic strata, the outer limit of shelf strata, and various other elements appear

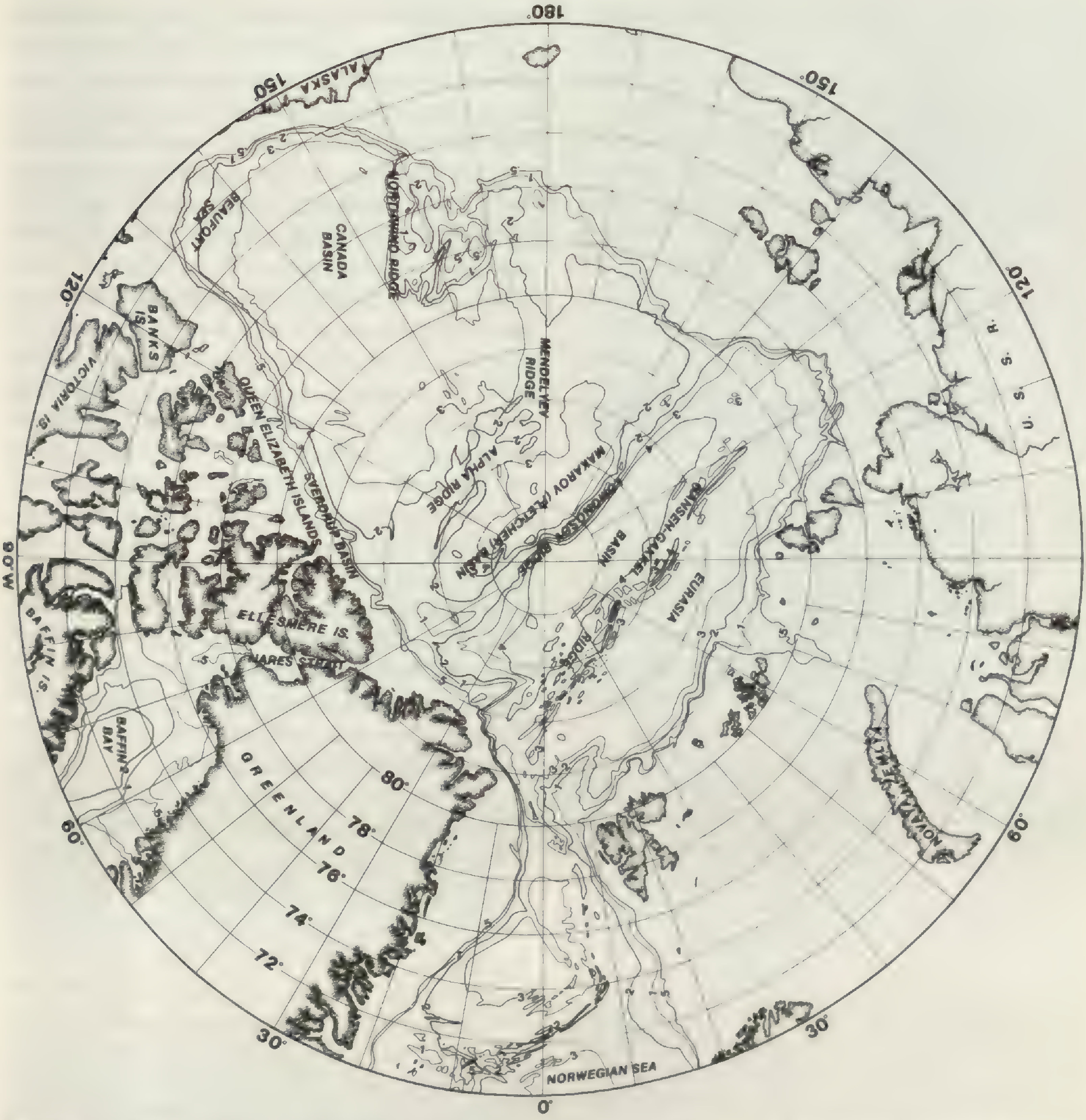

FIGURE 5. Bathymetry of the Arctic Ocean. Contour interval 1 km, with an additional contour at 0.5 km. Reproduced, with permission, from Taylor, Kovacs, Vogt and Johnson (1981, fig. 1a).

to me to accord with left slip of about 250 km along the strait, just as Wegener inferred long ago.

Nares Strait approximates a segment of a great circle. It is not a small circle to any likely Euler pole of relative rotation between Greenland and Canada, and hence must have changed in shape, position, or orientation relative to spreading centers between Greenland and Canada as spreading progressed.

Northwest Passage fault. The aligned sounds, 50 to 100 km wide, of the Northwest Passage curve westward from the north end of Baffin Bay and separate the northern and southern islands of the Canadian Arctic Archipelago. The midline of these sounds approximates a small circle to a pole near 85°N, 95°W, so the passage may mark a strike-slip fault along which the northern islands have slipped relative to the rest of Canada. Published data on distribution of facies in the widespread Paleozoic platform strata are compatible with a left slip of as much as 200 km, but not with any right slip (cf. Daae & Rutgers, 1975, and Kerr, 1980; these authors, however, assumed zero strike slip). Longitudinal faulting and variably thick Cretaceous and Paleogene sedi-

mentation in the passage are shown by geophysical data (Daae & Rutgers, 1975), and extensional faulting (which I assume to be oblique) is indicated in the eastern sector (Kerr, 1980).

Kerr (1974, 1977) argued against young strike-slip faulting along the Northwest Passage because the compressional "Cornwallis foldbelt" trends directly across the passage and is of Devonian age. Although structures north and south of the passage are indeed approximately in line, I interpret the geologic maps of Bathurst and Cornwallis Islands (Kerr, 1974; Thorsteinsson & Kerr, 1968), north of the passage, to indicate that the structures there are in fact of Tertiary age, and hence do not constrain strike-slip faulting. For example, a tract of uppermost Cretaceous and lower Tertiary strata on Cornwallis Island (the "Intrepid Bay Graben" of Thorsteinsson & Kerr, 1968, who regarded the Tertiary deformation as extensional) consists of an asymmetric syncline of the young rocks, against the steep, west limb of which is faulted a complex anticline of lower Paleozoic strata. Such geometry characterizes compressional, not extensional, structures.

South of the Northwest Passage, north-trending compressional faults of the Boothia uplift break basement as well as cover rocks, and can be dated directly only as postdating Lower Devonian strata and as predating highest Cretaceous strata (e.g., Miall & Kerr, 1977). That an upland was growing within the belt in mid Paleozoic time is indicated, however, by coarse clastic Upper Silurian and Lower Devonian sediments shed from it both to east and west (Miall & Gibling, 1978). No analogous upland is shown by correlative strata north of the passage, where dominantly carbonate rocks accumulated during this stratigraphic interval, platform conditions to the southeast giving way northwestward to continental-shelf ones. The lack of present continuity may be a result of post-Devonian faulting along the Northwest Passage, and the anticipated northern continuation of the upland and derivative clastics may now be hidden beneath younger strata and the sea farther west.

RECONSTRUCTION OF CANADA AND GREENLAND

If Baffin Island be rotated back to its pre-Cretaceous position as proposed previously, and southern West Greenland be brought back against Labrador in accord with the well-constrained magnetic-anomaly patterns of the Labrador Basin, the northern part of West Greenland is brought against Baffin Island in a reasonable fit (Fig. 4). The total motion of the south tip of Greenland, relative to mainland Canada, that is indicated by this reconstruction is about 800 km in northeastward direction. The motion reversed corresponds to a counterclockwise rotation of about 9° of Greenland relative to mainland Canada, about an Euler pole near 65°N, 140°W in a Canadian reference frame.

This reconstruction of Greenland, Baffin Island, and Canada is possible only if there is left slip on both Nares Strait and Northwest Passage faults. The specific reconstruction requires about 300 km of left slip through Nares Strait (compared to the best geologic value of about 250 km), and about 200 km of left slip along the Northwest Passage. The reconstruction also requires that the Northwest Passage and Nares Strait fault boundaries of the northern Arctic Islands (Queen Elizabeth Islands) have rotated toward one another about 5°, about the point of their intersection; the predicted northwest-increasing crustal shortening is presumed to be taken up by the northwest-widening belt of Cretaceous and early Tertiary folding in the islands.

TECTONICS OF THE ALASKAN REGION

The west limit of continental crust, as defined by the presence of continental-shelf strata and by other criteria, that was part of North America in early and middle Paleozoic time trends northwestward in interior British Columbia and southern Yukon, thence northward through northern Yukon to the Arctic Ocean. All land now to the west of this, including nearly all of Alaska, probably was added tectonically to the continent during Devonian and younger time. Diverse rotations and strike-slip motions have accompanied the tectonic accretion. The complexity of the collage increases northwestward, and comprehension of its evolution decreases correspondingly (e.g., Jones & Silberling, 1979; Jones et al., 1982; Monger et al., 1982; Tipper et al., 1981). A large part of the collage was assembled (although with grossly different configuration than it has now) before the middle of Cretaceous time. I will treat it here in only cursory fashion.

OPENING OF THE CANADA BASIN

The oceanic Canada Basin, north of Alaska and western Canada (Fig. 5), was formed by Mesozoic spreading, although the specific geometry

and timing of that spreading are poorly constrained. Interpretations have varied widely in detail but in general have advocated either that northern Alaska rotated counterclockwise away from Arctic Canada, as though about a pivot in the Mackenzie Delta region (e.g., Grantz et al., 1979), or that much of Alaska slid southwestward past Arctic Canada, the ocean opening behind it (e.g., Norris & Yorath, 1981). I strongly favor the rotation option. Magnetic-anomaly patterns of the Canada Basin are irregular (unlike the tidy, symmetrical anomalies of the Eurasia Basin; Fig. 6), and can at the present level of knowledge be fitted to either rotation or sliding models (Vogt et al., 1982). The onshore and offshore geology and geophysics of northern Alaska and northwestern Canada indicate that rifting premonitory to opening of the Canada Basin had begun by Early Jurassic time, and that an ocean of undefined width was present at least as early as late Early Cretaceous time (e.g., Grantz et al., 1979; Miall, 1979; Young et al., 1976). The magnetic anomalies of the basin were inferred by Vogt et al. (1982) to date the ocean floor as having formed largely within Late Jurassic and Early Cretaceous time.

The Canada Basin apparently is largely or entirely older than the Late Cretaceous and Cenozoic spreading and transform faulting by which the Eurasia Basin, Arctic Atlantic, Labrador Sea, and Baffin Bay were opened.

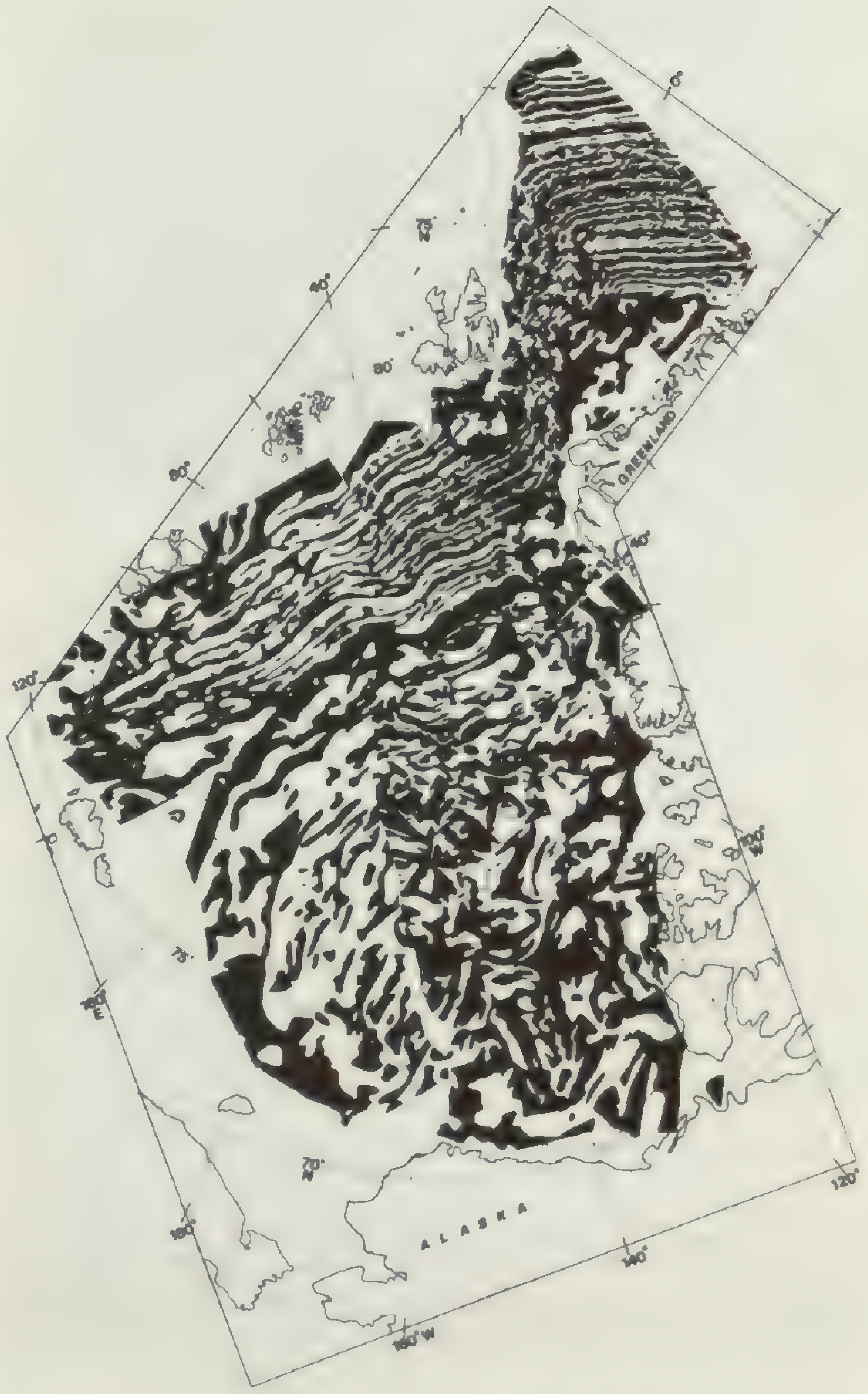

FIGURE 6. Magnetic anomalies of the Arctic Ocean and the northern Greenland-Norwegian Sea, showing medium-length anomalies greater than (black) and less than (white) the global magnetic reference field. The discontinuity near 160°W–60°E presents different data-reduction methods for the Soviet data, on the Eurasian side, and the generally more detailed U.S. Navy and Canadian data. Reproduced, with permission, from Vogt, Bernero, Kovacs and Taylor (1981, fig. 2).

ROTATION OF NORTHERN ALASKA

The Paleozoic and early Mesozoic geology of northern Alaska—the Brooks Range and North Slope—and adjacent northern Yukon Territory (e.g., Dillon et al., 1980; Grantz et al., 1979; Norris & Yorath, 1981) is compatible with the morphologically reasonable rotation of that region 65° counterclockwise away from the Canadian Arctic Islands (cf. Grantz et al., 1979). In the latter region, three major tectonic and lithologic or stratigraphic terranes trend generally west-southwestward to westward in the Queen Elizabeth Islands to oblique truncations against the margin of the Canada Basin. Analogous terranes in northern Alaska can be explained as rotated sectors of the same terranes. One assemblage consists of Mississippian through lower Mesozoic strata (in the Canadian Arctic, the Sverdrup Basin fill) lying unconformably on older complexes. The other two shared assemblages are pre-Mississippian. The southern one in the Canadian Arctic is a tract about 150 km wide of contorted and low-grade-metamorphosed upper Precambrian(?) through Silurian deep-water strata (e.g., Trettin et al., 1979). This terrane lies north of the continental-shelf assemblage of correlative shallow-water materials, deposited on North American crust. I interpret the deep-water materials to be sediments of the continental slope, continental rise, and abyssal plain, crumpled together while oceanic lithosphere beneath them was being subducted beneath an advancing northern landmass in Devonian time. Analogous materials in the northern part of the Alaska-northwest Yukon region are exposed in the Romanzof and other uplifts and are known also in the subsurface along the north coast. The north-

ern terrane in the Canadian Arctic is an assemblage of continental and oceanic crystalline and sedimentary rocks, of late Precambrian to Devonian ages (e.g., Trettin, 1982), which record poorly understood Devonian and older plate convergence and tectonic accretion. Equivalents of this northern Canadian Arctic assemblage appear to be represented by the Devonian and older terrane of the southern Brooks Range and nearby Yukon Territory.

CENTRAL AND SOUTHERN ALASKA

Alaska south of the Brooks Range consists of diverse terranes, some crustally oceanic and some continental, that have moved long distances with regard to the Brooks Range, mainland North America, and each other. The terranes are variously of Paleozoic, Mesozoic, and Cenozoic ages, but their present juxtapositions and configurations are primarily products of Cretaceous and Cenozoic subduction, strike-slip faulting, and oroclinal folding. Many terranes, sutures, and magmatic arcs have been identified, with varying levels of confidence, and fragmentary histories deduced; but any attempt at statewide palinspastic reconstructions for Cretaceous and early Paleogene configurations could be at present only quite speculative.

A large part of central and southern Alaska was nevertheless structurally part of North America by Late Cretaceous time. The suturing of the large Yukon-Koyukuk terrane, apparently an oceanic island arc, to the south edge of the Brooks Range occurred late in Early Cretaceous time. Before then, various terranes now farther south in Alaska were attached to the continent, but at positions farther southeast along the Cordillera; they slid northwestward to their present positions to form an increasingly wide Alaska.

The Aleutian Trench marks the present south margin of the Alaskan plate. Pacific oceanic lithosphere is moving relatively northwestward and subducting beneath Alaska and the Bering Sea. Alaska is widening as oceanic materials are scraped off into the accretionary wedge at its leading edge.

TECTONICS OF NORTHEASTERN EURASIA

The northern part of mainland Eurasia west of present latitude 162°E was assembled by the end of Jurassic time, although both major internal deformation and tectonic accretion continued in the east during the Cretaceous and Cenozoic (Churkin & Trexler, 1979; Dickinson, 1978; Fujita & Newberry, 1983; Hamilton, 1970; Takahashi, 1983; Tapponnier & Molnar, 1979[2]). It is likely that since about the middle of Cretaceous time, continuous crust of continental thickness (and hence, at least intermittently dry land) has joined mainland Eurasia and North America via the region of northeastern USSR and Alaska, although much doubt clouds specific palinspastic restorations.

PACIFIC MARGIN

Kamchatka Peninsula, the Koryak Highlands to the northeast of it, and the region northwest of the Koryaks, consist of a complex collage of accretionary and magmatic-arc terranes, 700 km wide, assembled primarily by Cretaceous and Cenozoic plate convergence. Subduction northwestward beneath the continent apparently began early in Cretaceous time, for Lower and Upper Cretaceous arc-magmatic rocks lie across the truncated and poorly understood components of older Mesozoic mainland terranes west of the Koryaks. Jurassic and Cretaceous fossils occur sparsely in the accretionary-wedge melanges that are widespread across most of the width of the collage; terranes of lower to upper Paleozoic rocks include fossils so foreign paleoclimatically to mainland northeast Asia as to require subduction of many thousands of kilometers of intervening oceanic lithosphere. Seamount and island-arc terranes are recognizable in the fragmentary Soviet descriptions, aided by analogy with northwestern North America. Melanges and Cretaceous and early Paleogene magmatic-arc rocks tend to become younger toward the Pacific, indicating a general sequence of tectonic accretion in that direction. Middle and upper Paleozoic components of mega-melange, including fragments of seamounts and atolls, are widespread in the Pacific half of the Koryak region, and as it is unlikely that any seafloor of this age

[2] Plate-tectonic interpretations of Soviet geology have come primarily from outside the Soviet Union, because plate concepts are all but lacking in the USSR. The papers cited above give references to Soviet publications. The following brief discussion is adapted from the references cited above and from my own reading of the Soviet literature regarding the far northeastern USSR.

was still unsubducted in Late Cretaceous time, tectonic assembly elsewhere is likely.

The Cretaceous magmatic arc of the Asian mainland margin, analogous to that west of the Koryak region, is present in Sikhote Alin, and the matching accretionary terrane is in Sakhalin, far west of the middle and late Cenozoic Hokkaido-Kuril-Kamchatka arc system. Dickinson (1978) inferred from regional geologic and geophysical relationships that a small continental crustal mass, represented now by the shallow part of the Sea of Okhotsk and perhaps by exposures in western Kamchatka, collided with the continental-margin subduction system in about Eocene time, and that subduction then broke through on the Pacific side of that added mass. Migration of the arc systems, and the opening of the Sea of Japan and the deep-water part of the Sea of Okhotsk, has occurred since.

ARCTIC MARGIN

The modern spreading center of the Nansen-Gakkel Ridge trends south-southeastward to the north edge of Eurasia, north of the Lena River delta (Figs. 5 and 6). The amount of Late Cretaceous and Cenozoic spreading decreases toward Eurasia but is still about 600 km at the Eurasian continental slope. One or several plate boundaries must connect this spreading center to past and present plate boundaries around the Pacific Ocean. A zone of diffuse seismicity continuing southeastward through the Lena River region to the Sea of Okhotsk presumably represents the modern boundary along which extension decreases southeastward between Eurasian and North American plates (Chapman & Solomon, 1976). Spreading within the region of the seismic zone cannot be great enough, however, to account for more than a small part of the total motion needed, for this mainland region is topographically high and is not conspicuously rifted.

One or more other plate boundaries, distinct or diffuse and now inactive seismically, must lie within the onshore or offshore region of Arctic Siberia. The most conspicuous geologic boundary onshore in the region is that trending east-southwestward relative to mainland Eurasia. Alternatively, perhaps, the broad lowlands of Arctic Siberia, undergoing active sedimentation between the Lena River and about 160°E, mark a zone of distributed crustal extension, offset from the modern seismic zone (cf. Chapman & Solomon, 1976).

BERING SEA REGION

The crust beneath the deep southwestern half of the Bering Sea, inside the Aleutian island arc, is oceanic, but that of the northeastern half is of continental thickness. Although now covered by shallow water, much of this latter half undoubtedly stood above sea level during much of its history.

Two broad geologic provinces can be recognized from geophysical and geologic data from the Bering Sea continental shelf and its margins. In the north, the terrane that includes the Brooks Range of northern Alaska inflects southward to form the Seward Peninsula of northwest Alaska, and thence trends westward through St. Lawrence Island to northeastern Chukotsk Peninsula (e.g., Patton & Tailleur, 1977). In the south is the broad terrane of accretionary geology and magmatic arcs connecting southwest Alaska and the northeast Koryak-southwest Chukotka region, probably consolidated mostly in Cretaceous and early Paleogene time (Csetjey et al., 1971; Marlow et al., 1976; Moore, 1972; Patton et al., 1976; Pratt et al., 1972). The accretionary and arc-magmatic history of the present shelf region ended in latest Cretaceous or very early Tertiary time, when subduction northward beneath the shelf region ceased.

The modern boundary between the Pacific and North American plates south of the Bering Sea is the Aleutian trench, which curves from southwest mainland Alaska to a trench-trench junction off Kamchatka. The Aleutian island arc has been active only since early or middle Eocene time; oceanic lithosphere between the Aleutians and the Bering continental slope probably is a trapped bit of Mesozoic ocean floor (Cooper et al., 1977) but might instead have formed in early Cenozoic time behind migrating island arcs (Langseth et al., 1980). Curving from the north side of the central Aleutian arc to the Koryak region are the Bowers and Shirshov submarine ridges—segments of a fossil arc beneath which subduction was southward (Cooper et al., 1981). Various explanations (e.g., Ben-Avraham & Cooper, 1981) have been proposed for the evolution of this complex submarine region. The most promising is one communicated to me by Dan M. Worrall, who integrated offshore geo-

physical data with onshore geological information. Worrall inferred that a northward-migrating, north-facing Bowers-Shirshov island arc collided with a south-facing Bering-Koryak Highlands continent-margin trench system in early Eocene time. He also inferred that both of these systems were abandoned when the Aleutian subduction system broke through the oceanic plate to the south, trapping Mesozoic oceanic crust to the north of it.

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HOLARCTIC LANDMASS REARRANGEMENT, COSMIC EVENTS, AND CENOZOIC TERRESTRIAL ORGANISMS

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ABSTRACT

Rearrangement of landmass configurations has profoundly affected the evolution of mammals and other organisms in the Northern Hemisphere. At the north end of the Atlantic Ocean, evidence is very strong for a now sundered landmass of Euramerica. This landmass existed toward the end of the Paleocene but began to separate into at least two landmasses in early Ypresian time at the beginning of the Eocene. Throughout most of the Eocene, Western Europe south of the Baltic Sea remained fragmented and separate from both Asia and the part of Europe and the attached Barents Shelf that lies north of the Baltic. Northern Scandinavia may have been essentially a peninsula of North America until the end of Eocene time. Thus at the end of the Paleocene and until some point very early in the Eocene, *two* land bridges may have simultaneously connected North America with separate parts of Europe across the north end of the Atlantic: one dominated by compression in the Greenland/Svalbard area plus any excess lava pile generated by early activity of the Yermak hotspot northwest of Spitsbergen, the other by the early activities of the Icelandic hotspot. Possibly a connection from western Asia and Europe to the northeastern end of North America existed at about 37 million years ago (Ma) through the combined activities of the Yermak hotspot, waning compression between Greenland and Svalbard, and the drying of Eurasian seaways. Throughout nearly all of the Cenozoic a land connection between Asia and Alaska existed at the Bering Strait, but the paleolatitude of the Bering Bridge was initially high and climate must have exerted a strong filtering action on mammals and other terrestrial organisms. It is possible, but only weakly supported on geological grounds, that a second northern Pacific bridge between Asia and North America existed via the Aleutians at the time the Kula Ridge was subducted. Other rearrangements that have strongly affected the composition of northern mammalian faunas and presumably would have affected many other organisms as well have been the reconnection of South America to North America in the Pliocene, the collision of India with Asia in the early Cenozoic (possibly earlier), and various Tethyan microplate transfers. Although paleobotanists and others have sometimes suggested that the warm polar climates of the early Cenozoic were the result of a lower mean spin axis obliquity of the Earth than the present 23.5°, no one has explained adequately how mean spin axis obliquity can be permanently changed significantly in the Cenozoic, where the necessary force would come from to shift it, how such a force would be coupled to the Earth, or how the resulting crustal heat would be dissipated. At present, therefore, known high latitude early Cenozoic environments of mammals and other organisms are not well understood, but a significant change of Earth's mean spin axis obliquity since the early Cenozoic is evidently out of the question. A catastrophic theory of Apollo-class asteroid impact at supposedly 35 Ma has recently been invoked to explain major Eocene/Oligocene faunal turn-over. However, major turn-over in both the marine and terrestrial realms occurred well before 35 Ma in both Europe and North America, as did the "North American tectite strewn field." Several such fields exist, however. Under a stable continent rationale, concepts of corridors, filters, and sweepstakes routes were developed by the 1950s by G. G. Simpson. Under a mobile continent rationale additional paleogeographic concepts have been added since then, such as Noah's arks and grounded Viking funeral ships for colliding or coalescing terranes bearing respectively either living or fossil contents. In addition, vicariance biogeography, with its emphasis on congruent cladograms of both the genealogies of the biota and of the geologic history of various areas, has been born and is undergoing growing pains. To these concepts may be added the notions of escalator counterflow and escalator hopscotch, whereby the existence of archaic elements of a biota can be reconciled with their presence on young mid-ocean-ridge islands like Iceland or mid-plate volcanic edifices such as those of the Hawaiian-Emperor chain. The retreat from, and return to, continental coasts by island arcs affected by subduction zone jumps provides a geological mechanism for biological voyages to nowhere and return, as would happen if the landmass of the volcanic arc separated from its parent continent, remained for a while in isolation, and then once more contacted the continent. Vicariant biotas produced by such means and nurtured in isolation would thus eventually be passively returned to contiguity with the parent continent. A certain amount of caution is called for before one should invoke far-traveled tectonic blocks, such as those plastered against the present shores of the North Pacific, as carriers of vicariant biota, now endemic to a terrane embedded in a foreign land. Before accepting such a block as a possible carrier of a terrestrial or even shallow water marine biota, it is important to determine if the block possesses continental or oceanic tectonic basement. Was the surface of the block always above sea level? Were its organisms transported only

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as fossils? Are the proposed vicariant sister groups at reasonable taxonomic levels in view of the time of tectonic transport of the block while in isolation? A parsimonious approach to all natural history, not merely biology, is necessary. Ad hoc hypotheses should be held to a minimum. The expanding Earth hypothesis is discounted as an explanation of discernible late Phanerozoic biogeographic pattern. Studies of mammalian diversity based on the fossil record have often been biased by tacit assumptions that biostratigraphic units have represented aliquot divisions of time. Calibration of mammalian biostratigraphy is under way, but until the subject is more advanced, published diversity/time relations should be taken with a grain of salt.

Authors of invited papers like this one are usually given the title of their paper, covering subject matter that the symposiarch hopes will somehow be dealt with adequately. However, the task usually proves to be overwhelming and the beleaguered author, nearly always at the last minute, produces instead a manuscript entitled "Problems of such and such." The author is then off the hook and able to postpone the real work. The "definitive effort" can always be written sometime next year. However, this paper is frankly such a preliminary effort even though it is longer than I would like it to be. In it I try to get at some of the main points in a vast subject in which I have taken some interest over the years, but it is aimed at an audience whose knowledge of vertebrate paleontology or modern geology is not necessarily very extensive and who might find a documented review useful. To me it seems obvious that some of the physical changes in the world that either have or might have affected the distribution of mammals in both space and time would also in some way affect much of the rest of the planet's biota. Our world has had a single history, which we try to decipher from a mixture of signal and noise coming from many sources of potential evidence. With regard to spatial distribution, the signal has in part been generated by geological processes and the noise in part by biological random dispersal and sampling errors. Although what follows is primarily a distillation from geology and mammalian vertebrate paleontology, the consequences are testable within other fields, such as botany and non-mammalian zoology. Indeed, the biological data can be used to test geological notions about the position and timing of continental interconnections, epicontinental seaway barriers, and so on. Geologists have much to learn from biologists, provided that the formulations of the biologists are well-founded.

A Mobile Garden of Eden

Early attempts to discuss the relationships of the vertebrates of the Northern Hemisphere, like those concerning plants or invertebrates, were necessarily based on the living biota alone and were made on the assumption that the geography of the Northern Hemisphere has always been more or less the same as it is now, give or take a seaway here or there, a shift in a coastline, or a cyclic change in climate (Dana, 1847, 1863). The Sclaters' (1899) and other nineteenth century authors' realms, regions, and so forth were based on such a foundation (de Beaufort, 1951; Simpson, 1953, 1965; Uvardy, 1975; Nelson & Platnick, 1981).

Gradually, however, the richness of the Recent data has been supplemented by an increasing knowledge of the vertebrate fossil record of various parts of the Earth. The geologic history of the world, in part dated by the fossil record and in part dated by other means, has become increasingly well known, spectacularly so in the last few years of intense effort associated with the plate tectonic revolution in geology.

But our paleontological knowledge of fossil vertebrates has not grown uniformly or smoothly. Indeed, the way our knowledge has grown has caused a bias in the results, partly because of the apparent randomness of discovery and partly because the efforts have largely emanated first from Europe, then from America, and finally from Asia and northern Africa. Thus, as time has passed, perspectives have shifted radically. At first, Europe was taken as an adequate sample of Holarctica. The evolution of horses, for instance, was believed to be a continuity represented in the European record by Eocene *Palaeotherium*, Miocene *Anchitherium* and *Hipparion*, and finally Pleistocene and living *Equus* (Huxley, 1872; Kowalevsky, 1873). However, the principal scene of equid evolution was elsewhere and the European record is now seen to be discontinuous, the result of repeated immigration to Europe of closely related animals rather than the product of our sparse temporal sampling of a single indigenous evolving lineage. Much the same may be said of camels, elephants, rhinoceroses, and many other groups of mammals.

Important as the European record was (and still is) for deciphering the Cenozoic vertebrate record of Holarctica, it suffers from several profound defects. For instance, there is no record of terrestrial Tertiary fossil tetrapods anywhere from the whole Fennoscandian northwest end of Europe, an area including Sweden, Norway, and the formerly subaerial Barents Shelf that lies in the Arctic between them and Svalbard. Another difficulty with the European Cenozoic record is that, until very recently (Godfriaux & Thaler, 1972; Thaler, 1977; Vianey-Liaud, 1979), there has been no record of medial or early Paleocene terrestrial vertebrates in Europe.

Starting in the 1870s, an explosive phase in the geological and paleontological exploration of the North American West began. This work soon produced an apparently much more continuous view of the evolution of various mammalian groups than had come to light in Europe other than for obvious European endemics such as doormice, certain kinds of artiodactyls, or dimylid insectivores, to name a few random mammalian examples. In North America, furthermore, terrestrial Paleocene sedimentary rocks turned out to be more completely represented than in Europe. Until recent discoveries, the terrestrial early or medial Paleocene fauna was represented solely in North America, where the land-laid deposits of the Rocky Mountain area of the United States and Canada supplied abundant and fairly well preserved fossil remains representing the earlier parts of the Paleocene. It was natural, then, that this North American terrestrial Paleocene sequence of faunal assemblages came to be regarded tacitly as representative of the ancestry of younger faunas on many continents, just as Europe had once been regarded as such a source. The Cenozoic Garden of Eden had shifted from Paris, France, to western North America, never to return.

But as the North American terrestrial vertebrate record was filled in by the efforts of E. D. Cope, O. C. Marsh, W. D. Matthew, and their successors, several important discontinuities appeared and some biogeographically disturbing alliances began to loom. Although a much more continuous record of certain groups, such as the famous horse sequence, was established in North America, a break between the American Eocene and Oligocene became obvious from the mammalian record (Wilson, 1980). Also, the source of several floods of latest Paleocene and/or early Eocene immigrants (Rose, 1981) into known fossil-producing areas of both North America and Europe from somewhere else became an increasingly vexatious problem. Furthermore, known North American late Cretaceous therian mammals did not appear to be ancestral to most Cenozoic forms.

For these reasons, northern Asia came to be regarded as the likely true Garden of Eden, where, if the record of remote Central Asia could just be sampled, all would become clear. Professor Henry Fairfield Osborn of Columbia University and the American Museum of Natural History held the firm belief, as did most of his associates, that the northern Asian ("Central Asian") record held the answers to the origin of various northern groups, including our own ancestry among the higher primates (Osborn, 1923a, 1923b). Osborn's view was responsible in large part for the mounting of the Central Asiatic Expeditions, a series of explorations in China and Mongolia that held the scientific spotlight in the field of natural history in the 1920s and whose spectacular labors filled in for the first time much of the Cretaceous, Eocene, Oligocene, and late Miocene terrestrial history of Mongolia and northern China. In Central Asia Osborn expected to find the ancestors of various rootless lineages of vertebrates known from Europe and North America. Given the assumptions of a stable-continent framework that prevailed in North American paleogeography in those days, what could be more natural than to find such links on the geographically intermediate landmass of Asia, half way between North America and Europe?

Early Cenozoic Holarctic Rearrangement

But, the northern Asian record for the early Cenozoic turned out to be a disappointment for ancestor seekers. Instead, as so often happens in science, a whole new series of problems arose (Szalay & McKenna, 1971; Fox, 1978). In place of ancestors, the Mongolian and Chinese early Cenozoic in many, even most, instances produced a new endemic cast of characters wholly unexpected in the terrestrial deposits of what was supposed to have been a continuous corridor (Simpson, 1943, 1953) connecting North America across Asia all the way to Europe. More recent collecting in the Paleocene of China has lent an even more peculiar aspect to early southeastern

Asian terrestrial faunas (Li & Ting, 1983). For instance, early primates, common enough in the North American and European Paleocene, are thus far completely absent from the Chinese Paleocene with only one possible but disputed exception, *Petrolemur*. Primates apparently reached eastern Asia only at the very beginning of the Eocene (Dashzeveg & McKenna, 1977). Multituberculates are also totally unrepresented in the known Chinese Paleocene, although they were previously abundant in the Mongolian Cretaceous and occurred again in Chinese and Mongolian assemblages at the very beginning of the Eocene. In place of these primates and multituberculates, Chinese Paleocene faunas supply us with a flood of new taxa that most Western paleontologists have found bewildering in variety and difficult to place in the scheme of things. In facile retrospect, clearly something was wrong and the flaw surely could have been spotted in the 1920s or 1930s had not the stable-continent rationale prevailed (Simpson, 1953, 1965).

What I refer to, of course, is that landmass interconnection within Holarctica in the early Cenozoic was arranged a bit differently from the familiar geography of the present day and of the Pleistocene (Wolfson, 1949; Nelson, 1973; McKenna, 1983). In the early Cenozoic, western Europe south of the Baltic Sea area and also the Fennoscandian shield of northwestern Europe north of the Baltic were for a time separately connected to North America by parallel routes around the north end of the Atlantic Ocean. Geological and paleontological evidence is more consistent with this reconstruction than one favoring an indirect connection by way of continuous land from northwestern North America to eastern Asia and then from western Asia to various parts of Europe. A continuous and habitable land connection from France and the British Isles to America via the Greenland-Scotland Ridge was a reality in the late Paleocene and earliest Eocene; most of the route, as far east as Iceland, may still have been intact above sea level as late as the Miocene (McKenna, 1975, 1983) although at least one break in land continuity must have been present as early in the Eocene as some point in Ypresian time. North of the Greenland-Scotland Ridge, a second connection between Greenland and Fennoscandia may have been possible throughout much of the Eocene because of compression between Svalbard and Greenland during the Eocene (Lowell, 1972) and possibly because of the early activity of the Yermak hotspot beginning at about 40 million years ago (Ma) (Batten et al., 1981).

Meanwhile, Asia was difficult to reach directly from North America or vice versa, not because of the lack of a land connection, but because the ancient land continuity between northeastern Siberia and Alaska was then at very high paleolatitudes (Wolfson, 1949). Until the end of the Eocene, marine barriers existed between central Asia and *western* Europe south of the Baltic, preventing terrestrial organisms of France, England, Belgium, Spain, and Portugal from reaching Asia from the west and forcing any dry-land dispersal of such forms in the late Paleocene or early Eocene to take place via the Greenland-Scotland Ridge, the eastern Arctic, and the north shore of the Pacific by way of Alaska and eastern Siberia. Russian authors have sometimes claimed that the Turgai Strait broke down in the early Eocene and permitted Eurasian transfers to take place via the so-called Kustanai elevation (Novodvorskaja & Janovskaja, 1977) at the narrowest part of the Turgai Strait, but this connection, if it existed, would not have been a route connecting western Asia directly to western Europe south of the Baltic. Rather, a Turgai Bridge at the Kustanai elevation in the early Eocene would have connected Asia directly to Fennoscandia, from whence terrestrial organisms may have been able to reach the rest of the western Europe via a round-about dry-land route through Greenland and proto-Iceland. Dispersal in the opposite direction over the same route might have occurred as well. In the mid-Tertiary, southwestern Asia was apprently isolated from Europe (Jacobs et al., 1981; Heintz & Brunet, 1982).

The effects on the biota of this formerly very different geography of the northern world are profound, although even now they are not well understood. No longer, however, can it be said as, for instance, Darlington (1957: 606–607) did, that fossil mammals support the notion of permanent continental allegiances and permanent oceanic barriers. Rather, patterns of endemism shown by early Cenozoic Holarctic mammalian faunas are consistent with the paleogeography reconstructed by students of plate tectonics (McKenna, 1975, 1983).

The Early Cenozoic Pole Position

I have elsewhere summarized the rather scanty published data bearing on the position of the early Cenozoic rotational pole with regard to

TABLE 1. Position of early Cenozoic rotational pole with regard to North America (from McKenna, 1980a).

Age	Latitude N.	Longitude E.	Error	Author
60 Ma	75.9°	147.7°	—	Butler and Taylor, 1978
45 Ma	87°	169°	6°	Simpson and Cox, 1977
45 Ma	82°	170°	5°	Irving, 1979

North America (McKenna, 1980a). Various previous calculations yielded the results shown in Table 1.

Recently, these results have been upgraded by Harrison and Lindh (1982a: 1912, table 8; 1982b), utilizing a carefully conceived method of averaging and weighting data. Their results for a period covering the interval from about 80 to 20 Ma are shown in Table 2.

Harrison and Lindh (1982a) made a concerted effort to avoid inclusion of paleopolar data from displaced terranes of Western North America (Beck, 1980; Cox, 1980). Their results differ significantly concerning the 40 Ma paleopole of Briden et al. (1981), but the latter included data from the almost certainly rotated Twin Sisters dunite of the state of Washington (Beck, 1975). Harrison and Lindh removed the Twin Sisters dunite data and, using the method of Briden et al., obtained results close to their own (Harrison & Lindh, 1982a: 1910).

Thus, in the middle of the Eocene the averaged magnetic pole position, or in other words the position of the Earth's rotational axis, was relatively about 7° closer to the Bering Strait area than at present. Put another way, since the medial Eocene the lithosphere in the Bering area has moved away about 7° relative to the mean position of the Earth's spin axis.

It is also important to know the paleolatitude of Ellesmere Island in the early Cenozoic. Eocene fossil invertebrates, vertebrates, and deciduous plants are now known from that critical area of the northeastern Canadian high Arctic (Miall, 1981; West et al., 1981) and therefore these organisms yield information about the early Cenozoic environment there. At the time or times in the early Cenozoic when these organisms were capable of living on Ellesmere Island, the world's oceans were quite warm (Savin et al., 1975; Savin, 1977; Buchardt, 1978; Shackleton & Boersma, 1981) and poleward transport of heat by

TABLE 2. Position of early Cenozoic rotational pole with regard to North America (from Harrison & Lindh, 1982a, 1982b).

Median Age	Studies	Latitude N.	Longitude E.	Error
76.3 Ma	11	70.6°	195.1°	7.4°
67.9 Ma	18	76.6°	188.4°	5.6°
58.5 Ma	23	80.0°	183.8°	4.7°
48.3 Ma	26	83.1°	178.2°	3.5°
38.9 Ma	26	83.4°	165.4°	3.5°
30.4 Ma	29	84.7°	157.7°	3.6°
19.9 Ma	25	85.9°	151.1°	3.6°

oceanic currents and the atmosphere was evidently great. Ellesmere Island was at that time almost certainly located on the path between Canada and either of two bridges that separately connected Greenland with lands to the east. The paleolatitude of terrestrial Eocene fossil vertebrate-producing sites on Ellesmere Island, whose present coordinates are here taken for convenience as 78.75°N, 277.25°E, can be recalculated for 48.3 Ma using the following formula:

$$\text{Paleolat.} = \sin^{-1}[\sin \text{lat.}_s \sin \text{lat.}_p + \cos \text{lat.}_s \cdot \cos \text{lat.}_p \cos(\text{long.}_p - \text{long.}_s)].$$

In this formula, s = site and p = position of former rotational pole.

Such a calculation yields a medial Eocene paleolatitude for the terrestrial fossil-bearing sites: 75.9°, error 3.5°. This result is not significantly different from my previous paleolatitude calculation for the Ellesmere sites: 77.5°, error 6° (McKenna, 1980a), nor from their present latitude. If the paleopole position for 48.3 Ma determined by Harrison and Lindh is accepted, then the Eocene Ellesmere Island terrestrial biota would have lived at an angular distance of 14.1°, error 3.5°, from the spin axis, well within the Arctic Circle if the extent of the Arctic Circle was then the same as now. The path of polar relative motion between the rotational axis position and that of the Bering Strait area was approximately at a right angle to a line from the pole to the Ellesmere sites. For this reason the paleolatitude of Ellesmere Island has not changed significantly during the Cenozoic, while that of the Bering Strait area has decreased by about 7° since the medial Eocene and by a total of about 13° since the end of the Cretaceous. Thus, in the early Cenozoic, the Bering area was relatively much closer to the rotational pole than the Eurameri-

can connections at the north end of the Atlantic Ocean.

MEAN OBLIQUITY OF EARTH'S SPIN AXIS

Several authors, notably Allard (1948), Williams (1972, 1974), Wolfe (1977, 1978, 1980), and Xu (1980), have claimed on the basis of botanical and other indirect climatic evidence that the mean spin axis of the Earth was more nearly parallel to the axis of the Earth's orbit in the early Cenozoic than its current mean obliquity of 23°27′3″. This would mean that the radius of the Arctic Circle has increased since the early Cenozoic. Such a notion is attractive at first glance because it would have permitted nearly equal days and nights throughout the year in those times and would not have fatally disrupted photosynthesis. But there is a problem with the physics of this hypothesis. Mechanisms exist, of course, for moving a large part of the Earth with respect to another oppositely moving part or parts (Gold, 1955; Goldreich & Toomre, 1969; Jurdy, 1981), but a large extraterrestrial force operating over a long time would be required to affect the angular momentum vector *H*x of the entire Earth (Fisher, 1974: 4044). Except for orbital resonances that are not expected to affect Earth for another couple of billion years (Ward, 1982; Harris & Ward, 1982), no such enormous force capable of affecting Earth significantly in the Cenozoic is known. Moreover, were it to exist, no way is known to couple it to the Earth. The law of conservation of momentum stands in the way. Collisions with large, high-velocity comets or large, relatively low velocity asteroids would, of course, produce instantaneous effects as well as long-term ones, especially at very early times in the Earth's history (Clube & Napier, 1982), but by Cenozoic times such effects would have become negligible. An effect large enough to shift the axis instantaneously as much as 5° (Nafziger & Dachille, 1965) would have totally disrupted the life of our planet as well as its geology. Averaged over a long time, essentially random arrivals of large extraterrestrial bodies would affect the spin axis's orientation if enough such arrivals occurred. But if a long-term gradual shift of the mean obliquity of the Earth's spin axis with regard to the ecliptic had in fact occurred since the end of the Mesozoic, then one would expect that, in the much longer interval since the early Precambrian, the mean obliquity of the Earth's axis as well as those of most other large bodies in the solar system would have shifted so much that a random scatter of their mean inclination values would prevail. Such is not yet the case (McKenna, 1980a). Moreover, for the Earth at 850 Ma in the late Precambrian, obliquity calculated from growth features of stromatolites at one site was about 26.5° (Vanyo & Awramik, 1982), close to the present value and therefore evidence for long-term stability since the late Precambrian. True, only one site of that age has been investigated in this way so far, but the matter can easily be tested further.

One could also bring up the problem of how to dispose of the enormous amount of heat that would necessarily have been generated in a short time if a large extraterrestrial force was indeed applied rapidly, etc.

I am thus unconvinced by all indirect arguments claiming modification of mean obliquity with respect to the Cenozoic ecliptic that do not deal quantitatively with the required physics of the process (Ward, 1982). If empirical evidence of such an event were found, then physics would have to explain it, but thus far the arguments are indirect chains of reasoning based on conclusions about past climates that are in some cases themselves suspect.

From the preceding arguments I conclude that the Eocene climate of the areas where North America was connected to other northern landmasses was generally warm but necessarily seasonal, and that in general the North Atlantic connections would have been more hospitable than was the case at the north end of the Pacific.

THE GRANDE COUPURE

The Grande Coupure (Stehlin, 1909) is a strong break in western European faunal continuity that occurred between Ludian time (= Priabonian, latest Eocene) and Sannoisian time of the early Oligocene (= early Rupelian, Stampian, or Lattorfian of some authors. See Bosma, 1974; Brunet, 1975, 1977; Cavelier, 1976; Cavelier et al., 1981; Hartenberger, 1983; Berggren et al., in press).

The western European terrestrial Oligocene fauna shows a major turn-over following the Eocene, with many mammalian extinctions and also many mammalian introductions from elsewhere, mainly from Asia and southeastern Europe after the drying-up of certain eastern European seaways and the former Turgai Strait (Obik Sea). The latter had until then formed an

epicontinental water barrier between Asia and Europe nearly continuously since the Jurassic (McKenna, 1975; Heissig, 1979). A sharp decline in oceanic bottom water temperatures throughout the world occurred at the same time (Kennett & Shackleton, 1976; Corliss, 1979; Keigwin, 1980; Cavelier et al., 1981; Norris, 1982). Thierstein and Berger (1978), as well as Miller and Curry (1982), have argued that this temperature drop was caused by recombination of previously isolated brackish Arctic Ocean water with that of the world ocean, a sort of latter-day reincarnation of the Gartner and Keany (1978, 1979; see also Clark & Kitchell, 1979) Arctic spill-over model in which cold, low-salinity water from the Arctic mixed with that of the World Ocean. By contrast, Kennett and Shackleton related the event to the opening of the more distant Tasman Seaway as Australia separated from Antarctica.

In western Europe the Grande Coupure is important because on paleontologically parsimonious grounds it supports the existence of a large scale basal Oligocene terrestrial dispersal event, nearly simultaneous in geological terms. It must have affected far more organisms than just the mammals and those other organisms whose fossil record possesses high enough resolution to document its occurrence. In the marine Cenozoic rocks of the world, but especially in Tethyan Europe, faunal and floral changes are marked at the Eocene-Oligocene boundary, although many taxa cross it with little or no modification (Beckmann et al., 1981; Cavelier et al., 1981; Hubbard & Boulter, 1983).

Seventeen western European terrestrial mammalian genera whose last species became extinct at the Grande Coupure, between the Ludian and the Sannoisian (= between the equivalent marine Priabonian and the Stampian, sensu lato), constitute the following list (modified from Brunet, 1977):

Artiodactyla
- Choeropotamidae
  - *Choeropotamus*
- Xiphodontidae
  - *Xiphodon*
  - *Dichodon*
  - *Haplomeryx*
- Amphimerycidae
  - *Pseudamphimeryx*
- Anoplotheriidae
  - *Anoplotherium*
  - *Dacrytherium*

Creodonta
- Hyaenodontidae
  - *Pterodon*

Primates
- Adapidae
  - *Adapis*
- Microchoeridae
  - *Microchoerus*
  - *Pseudoloris*

"Insectivora"
  - *Amphidozotherium*
  - *Pseudorhynchocyon*

Rodentia
- Theridomyidae
  - *Oltinomys*
  - *Thalerimys*
  - *Patriotheridomys*

At the same time, twenty previously unheralded new occurrences in western Europe, most of which appear to have originated elsewhere, include species of the following mammalian genera (modified on the basis of Brunet, 1977):

Perissodactyla
- Rhinocerotoidea
  - *Eggysodon* (*Ronzotherium* and *Cadurcotherium* followed almost immediately thereafter, prior to the Ronzon Fauna)

Artiodactyla
- Entelodontidae
  - *Entelodon*
- Anthracotheriidae
  - *Bothriodon*
- Gelocidae
  - *Gelocus*

Carnivora
  - *Amphicynodon*
  - *Eusmilus*

Insectivora
- Erinaceinae
  - ?*Amphechinus*
- Plesiosoricidae
  - *Butselia*
- Soricidae
  - ?*Quercysorex*

Chiroptera
- Vespertilionidae
  - *Myotis* (but the family was in Europe earlier)

Lagomorpha
  - *Desmatolagus* (possibly not the same genus as the Asiatic form)
  - ?*Shamolagus*

Rodentia
- Aplodontidae
  - *Sciurodon*
- Theridomyidae
  - *Sciuromys* (probably not from elsewhere, however)
- Gliridae
  - *Peridyromys* (probably not from elsewhere, however)
- Sciuridae
  - *Palaeosciurus*
- Cricetidae
  - *Eucricetodon*
  - *Heterocricetodon*

Eomyidae
Omegodus
Castoridae
Steneofiber

Passing through the western European Grande Coupure with no more than species-level adjustments were the following twenty-five lines of mammals (Brunet, 1977, with modification):

Perissodactyla
Palaeotherium
Plagiolophus
Artiodactyla
Dichobunidae
Dichobune
Cebochoeridae
Cebochoerus
Anoplotheriidae
Diplobune
Tapirulus
Cainotheriidae
Oxacron
Paroxacron
Creodonta
Hyaenodontidae
Hyaenodon
Carnivora
Canidae
Cynodictis
"Insectivora"
Nyctitheriidae
(undescribed taxon)
Talpidae
Geotrypus
Myxomygale
Pantolestidae
Dyspterna
Apatotheria
Apatemyidae
Heterohyus
Chiroptera
Rhinolophidae
Rhinolophus sensu lato
Paraphyllophora
Palaeophyllophora
Emballonuridae
Vespertiliavus
Molossidae
Tadarida
Rodentia
Theridomyidae
Theridomys
Blainvillimys
Pseudoltinomys
Elfomys
Gliridae
Gliravus

Well along in the early Oligocene, at the end of the Sannoisian (= earliest Stampian, sensu lato), between the levels represented by the late Sannoisian Ronzon and the early Stampian Villebramar faunas, another, less important event seems to characterize the western European Oligocene faunal sequence. Seven mammalian lines becoming extinct at this time were:

Perissodactyla
Pseudopalaeotherium
Plagiolophus minor (a formerly long-lived species quite separate from *Plagiolophus fraasi*)
Artiodactyla
Anthracotheriidae
Bothriodon
Carnivora
Canidae
Cynodictis (may have given rise to later *Haplocyon*)
"Insectivora"
Darbonetus
Dyspterna
Cryptopithecus

Six mammalian immigrants appear to be the following:

Artiodactyla
Suidae
Palaeochoerus (perhaps earlier)
Anthracotheriidae
Anthracotherium
Gelocidae
Lophiomeryx
Hypertragulidae
Bachitherium
Carnivora
Mustelidae
Plesictis
Nimravidae
Nimravus (perhaps earlier)

Passing through the event with little more than species adjustments were thirty-nine mammalian lines:

Perissodactyla
Plagiolophus
Cadurcotherium
Eggysodon
Ronzotherium
Artiodactyla
Dichobunidae
Dichobune
Entelodontidae
Entelodon
Anoplotheriidae
Diplobune
Cainotheriidae
Plesiomeryx
Caenomeryx
Gelocidae
Gelocus
Creodonta
Hyaenodontidae
Hyaenodon
Carnivora
Amphicynodontidae
Amphicynodon
Nimravidae
Eusmilus

"Insectivora"
  Nyctitheriidae
    (undescribed taxon)
  Talpidae
    Geotrypus
    Myxomygale
  Plesiosoricidae
    Butselia
  Soricidae
    ?*Quercysorex*
  Erinaceinae
    ?*Amphechinus*
Chiroptera
  Rhinolophidae
    Rhinolophus, sensu lato
    Paraphyllophora
    Palaeophyllophora
  Emballonuridae
    Vespertiliavus
  Molossidae
    Tadarida
  Vespertilionidae
    Myotis
Lagomorpha
    Desmatolagus
Rodentia
  Aplodontidae
    Sciurodon
  Theridomyidae
    Sciuromys
    Theridomys
    Blainvillimys
    Pseudoltinomys
    Elfomys
  Gliridae
    Gliravus
    Peridyromys
  Sciuridae
    Palaeosciurus
  Cricetidae
    Eucricetodon
    Heterocricetodon
  Eomyidae
    Omegodus
  Castoridae
    Steneofiber

It is interesting as well to compare western European mammalian faunal turn-over, or rather the lack of it, at an Eocene event just before the Grande Coupure. According to Brunet's (1977) data, here slightly updated, there were few extinctions or introductions in the time immediately preceding the Grande Coupure. Thus, between the levels represented by Montmartre in the Paris Basin and St. Capraise d'Eymet in the Aquitaine Basin of France, these intra-Eocene western European mammalian extinctions were limited to the perissodactyls *Anchilophus* and several species of *Palaeotherium*. Mammalian introductions to western Europe were confined to the "insectivores" *Amphidozotherium* and *Cryptopithecus*. In a similar but more detailed study of the Paleogene mammalian faunas of Quercy, France, Crochet et al. (1981) found no dramatic breaks until the Grande Coupure. The same progressive, rather than sudden, change appears to have characterized the evolution of western European floras in the Eocene (Collinson et al., 1981). By "progressive" I do not necessarily wish to imply "gradual" or "smooth." What I do wish to indicate is that nothing spectacular occurred until the Grande Coupure.

TABLE 3. Summary of western European late Eocene and early Oligocene mammals.

Time Planes	Extinctions	New Occurrences	Unaffected
Earliest/Early Stampian	7	6	39
Grande Coupure (38 Ma)	17	20	25
Montmartre/St. Capraise d'Eymet	5	2	41

These lists of western European late Eocene and early Oligocene mammals are summarized in Table 3.

Note that in all three levels of discernible mammalian faunal change there were more western European mammalian lineages passing through the event in situ with little or no change than the number becoming extinct. Known pre-Grande Coupure, unheralded, new mammalian additions were limited in the late Eocene to *Amphidozotherium* and *Cryptopithecus*, whose affinities are poorly understood but are not necessarily Asian or American except through remote ancestry. Of the new western European occurrences at the time of the Grande Coupure, however, nearly all had obvious Asian or American affinities or both. Exceptions or possible exceptions are the artiodactyl *Gelocus*, the theridomyid rodent *Sciuromys*, and the glirid rodent *Peridyromys*. Most or all of the new occurrences at the somewhat later earliest/early Stampian event at the end of the Sannoisian in the Oligocene also possessed Asian and/or American affinities. These new occurrences may therefore legitimately be labeled *arrivals*.

In the case of both the Grande Coupure and the later event at the end of the Sannoisian, the number of western European mammalian extinctions was about equal to the number of mammalian arrivals in each example. The Grande

Coupure, therefore, can be regarded as a biological event related to the advent of a dry-land connection from western Europe eastward to southeastern Europe and to Asia and beyond. The event is similar to what happened to South America's biota when connection to North America was established near the end of the Cenozoic (Webb, 1976; Marshall & Hecht, 1978; Marshall et al., 1982). In historical terms, it might be compared to the Oklahoma Land Rush of April 22, 1889, although I admit that fewer taxa were involved in the latter. All terrestrial organisms would have been affected, including, of course, plants, although one might suspect that many plants and some animals were able to cross the narrowing water barrier somewhat before it dried up completely. Repenning (1967) and Tedford (1970) have recommended that such biological invasions be made the basis of the beginning points of Mammalian Ages. Such a geographic change would also have had profound effects on various more distant marine environments and on climate. Indeed, the event is correlated by western European stratigraphers with the marine faunal turn-over between Priabonian and Stampian (sensu lato) faunas that is taken as the Eocene/Oligocene boundary. Cooling of oceanic bottom waters throughout the world occurred at the same time (Kennett & Shackleton, 1976), although in western Europe floristic evidence indicates that cooling of terrestrial environments had begun in the Eocene and was not particularly dramatic at the end of the Eocene (Collinson et al., 1981; but see Hubbard & Boulter, 1983). In the Arctic, however, the Oligocene temperature drop was more dramatic (Norris, 1982), suggesting as well that climatic zonation became more pronounced at the beginning of the Oligocene.

Connectedness of the Bering Land Bridge Area and the Spectre of an Aleutian Bridge

Although a brief stretch of shallow sea water presently interrupts land continuity between Asia and Alaska at the Bering Strait, a wide land connection formerly existed there (Scholl & Sainsbury, 1961), long before humans first used it in the Pleistocene. A dry land connection in prehistoric times has been a factor in anthropological dispersal theory since its original proposal by Fray Jose de Acosta in 1590 (Wilmsen, 1965). But, even before the Pleistocene, dry land had apparently existed in the Bering Strait area since the Mesozoic (Hopkins, 1967; Scholl et al., 1968; Churkin, 1972), with minor epicontinental transgressions occurring at the very end of the Cenozoic (Ostenso, 1968). For a time in the 1960s and 1970s late Miocene and even earlier Cenozoic seaways through the area were postulated (Mitchell, 1966; Durham & MacNeil, 1967), but further work has discounted such early incarnations in the Cenozoic of the modern Bering Strait (McKenna, 1983, and references cited therein).

Evidently, the *utilization* of this bridge by terrestrial organisms has been controlled primarily by climate, such as warm interglacials or warm periods that extended poleward like that of the medial Miocene (Addicott, 1969) before glaciation began (Bandy et al., 1969) or the warmer climate of the early Cenozoic and Mesozoic. As can be seen from the paleomagnetic information provided by Harrison and Lindh (1982a, 1982b), the site of the Bering Strait at the end of the Cretaceous was very close to the rotational pole and the area would have suffered whatever polar climatic extremes existed then. From the late Cretaceous onward, the Bering Bridge area has steadily retreated southward relative to the rotational pole. During the early Cenozoic the Bering area would have suffered longer winter darkness and a more extreme yearly climate than any of the then more southerly placed bridges connecting Canada to Greenland and parts of Europe. The Bering Bridge area has thus long acted as a filter, sometimes strong and sometimes weak, whose action has always been controlled primarily by daylight length and climate. During the Cenozoic, only toward the close of the Era was a short Beringian water gap added to the mix.

A possible second bridge between Asia and Alaska, via the Aleutian Island chain, has been suggested by DeLong et al. (1978), who pointed out that uplift under the Aleutian arc (Gates & Gibson, 1956) would have occurred at the time of subduction of the now-destroyed Kula Ridge, which was subducted under the Aleutian Trench. The latter may have jumped southward to its present position relative to the rest of Alaska at the end of the Cretaceous (Cooper et al., 1976), or it may have had a more southerly position (Marlow & Cooper, 1983). According to DeLong et al. (1978), the present Kamchatka Strait area at the west end of the modern Aleutians originated in the late Cenozoic. Unfortunately, the

exact position or time of subduction of the Kula Ridge is not known, having been estimated as occurring either in the late Paleocene to early Eocene (Hayes & Pitman, 1970; Byrne, 1979) or in the mid-Cenozoic about 30 ± 10 million years ago (Grow & Atwater, 1970; DeLong & McDowell, 1975). DeLong et al. (1978) opted for a time of emergence beginning about 42 Ma and ending at 15 Ma. Probably any possible continuity ended before 15 Ma because the Meiji sediment tongue, directly south of Kamchatka Strait, began to form in the early Miocene (Scholl et al., 1977). Utilizing Harrison and Lindh's (1982a) paleopole positions, I calculate that at 38.9 Ma the paleolatitude of both the eastern and western portals of the ancient Aleutian arc would have been at about 63°N, with the southernmost, central part of the arc at about 58°N, provided that the arc was not farther south as suggested in one of Marlow and Cooper's (1983) models.

If an Aleutian Bridge existed, it would have filtered any exchange of organisms between Alaska and Asia because its narrowness would have allowed few biotopes and because, to cross it, organisms would have required a distribution that included the restricted position of one of its portals. The climate of such an Aleutian Bridge, however, would presumably have been somewhat milder than that of the more northerly-positioned Bering Bridge. Moreover, the length of days and nights would have been slightly more equal throughout the year. Between the two bridges, the Bering Sea might well have been a fresh-water body for a time in the mid-Cenozoic, if indeed an Aleutian Bridge was a reality and blocked water exchange with the Pacific Ocean to the south. The Sea of Japan was briefly such a fresh water body near the end of the Miocene (Burckle & Akiba, 1978). Such a possibility in the Aleutian Basin could be tested by the drill. For the moment, a mid-Cenozoic Aleutian Bridge lying to the south of the Bering Bridge is an interesting but highly speculative possibility in need of further investigation.

Tectonic Flotsam

The tectonic history of the north end of the Pacific Ocean and its continental borders is becoming known rapidly, largely through paleomagnetic studies and through application of studies of the fates of the now-subducted Kula Plate and Kula Ridge as well as of the nearly swallowed Farallon Plate (Stone et al., 1982; Jones et al., 1982) and some oceanic plateaus (Ben-Avraham & Cooper, 1981). As Pacific Ocean floor has moved thousands of kilometers generally northward, many allochthonous small blocks associated with or affected by these plates have been added to the coasts of the bordering continents or subducted beneath them (Alvarez et al., 1980; Irving et al., 1980; McElhinny et al., 1981; Barron et al., 1981; McWilliams & Howell, 1982). The history of these collisions is largely a Mesozoic one, but chunks of Alaska and British Columbia have continued to move a thousand kilometers or more during the Cenozoic (Cowan, 1982; Marlow & Cooper, 1983) and various coastal blocks of North America have rotated clockwise (Beck & Plumley, 1980; Bates et al., 1981; Globerman et al., 1982) as the result of the generally northward motion of the Pacific oceanic floor and plate consumption along the West Coast (Packer & Stone, 1972; Stone & Packer, 1977; Cox, 1980; Drake, 1982). Rotations have also been observed along the Pacific coast of Asia.

Southwestern Alaska has been the site of tectonic unrest throughout the Cenozoic as various terranes have arrived from the south (Scholl et al., 1975). Essentially all of the terranes south of the Denali Fault were formed at sites many degrees to the south of their present position and have been mashed against the North American Plate as the Kula Plate and part of the Pacific Plate moved north to destruction under North America and eastern Asia. In contrast, Paleocene volcanics just north of the Denali Fault are magnetized with steep inclinations, indicating that they were formed in high latitudes (Plumley et al., 1982). Alaska north of the Denali Fault was in essentially its present position much earlier than terranes to the south (Sweeney, 1982). Thus, environmental information derived from Paleogene and Mesozoic floras south of the Denali fault system tells us not about ancient Alaska but about somewhere else.

Through the Tank of Sheep-Dip

It is tempting to envision some of these far-traveled small blocks as Noah's arks (McKenna, 1973), each bearing a biota whose affinities lie with some distant homeland either along the western shore of North America or across vast oceanic stretches. Indeed, many of the blocks were in the southern hemisphere as late as Ju-

rassic times (Stone et al., 1982). However, their arrival in the north from an ultimate source in "Pacifica" (Melville, 1981; Nur & Ben-Avraham, 1977, 1981, 1982), or from oceanic volcanic arcs or mid-plate volcanic edifices that had somehow become populated from elsewhere, was in most or all cases apparently too early to have had any discernible effect on the composition of Cenozoic vertebrate faunas of the north. Further, the various blocks may not have all come from the same place. Finally, most of the blocks seem to rest on oceanic basement (Ben-Avraham et al., 1981; Jones et al., 1982) and thus those that do were never initially part of *any* continent.

Possibly the biological effects of passive transport followed by merger of the tectonic substrate could be seen by analyzing patterns of endemism of organisms whose ancestors were affected by transoceanic transfer on the fragments that have ultimately come to rest in Alaska, Siberia, Japan, or British Columbia and the western coast of the United States. Such an analysis should proceed according to the method set forth by Rosen (1978) and by Nelson and Platnick (1978, 1981). But, as I have elsewhere (McKenna, 1981) pointed out, such blocks, if embedded in oceanic crust, would tend to sink as the ocean floor moved away from a generating ridge. The amount of such sinking is generally proportional to the square root of the time involved since the site was generated at the ridge crest (Sclater & Parsons, 1981), but for most "normal" ocean floor the depth with respect to time since plate generation is perhaps better represented by the formula:

$$d = 6{,}400 - 3{,}200e^{-t/62.8}$$

where d is the depth in meters and t is time in millions of years. This formula, developed by Parsons and Sclater (1977), has the advantage of yielding results that are asymptotic to a limiting water depth of 6,400 meters. After 70 million years of lateral motion, rocks once at the mid-oceanic generating ridge subside to within about 1,000 meters of such a depth. Small blocks of continental crust, aseismic ridges, guyots, or anomalous crust such as that of the present-day Ontong Java or Manihiki plateaus (Heezen et al., 1965; Nur & Ben-Avraham, 1982; Rogers, 1982) would rise higher than "normal" oceanic floor and thus would require the use of different constants in the equation. However, if such small blocks are to be invoked as Noah's arks, it must be shown how their surfaces could have remained continuously above sea level for the entire journey in order to avoid drowning their terrestrial inhabitants. Even photic zone inhabitants, for instance corals, would soon perish if in the course of their passive lateral transport they were carried to greater than shallow depths. At present, blocks like the Ontong Java, Manihiki and many other oceanic plateaus are, after all, either mostly or totally far below sea level.

Noah's Arks

Large blocks of sialic crust are another matter: we call them continents! India's northward flight away from the rest of Gondwanaland and its merger with Asia (Klootwijk & Peirce, 1979; Mitchell, 1981; Brookfield & Reynolds, 1981) is one example of a major Noah's ark transfer that was consummated some time either in the late Cretaceous or early Cenozoic prior to the medial Eocene (Maluski et al., 1982). The vicariant inhabitants of India that had resulted from its departure from other parts of Gondwanaland were largely swamped by dispersal on India's contact with Asia. Patterns of endemism that remain in India, however, point to a former Gondwana affinity of India, which is now crushed into and under the Himalayas and Tibet (Klootwijk & Bingham, 1980; Boulin, 1981; Gupta & Delany, 1981). Australia's and southern New Guinea's northward motion is well known (Wegener, 1924; Lam, 1934; LePichon & Heirtzler, 1968; Raven & Axelrod, 1974; Audley-Charles et al., 1981) and a collision with Asia is beginning (Hamilton, 1979; Coleman, 1980; Audley-Charles, 1981). South America's Cretaceous departure from Africa and its reconnection to the rest of the world via North America at the end of the Cenozoic is another example (Raven & Axelrod, 1975; Tarling, 1980; McKenna, 1980b; Vink, 1982). On a smaller scale, the many jostlings over short distances of mini- and micro-plates of the Tethyan area offer numerous possibilities for Noah's ark transfers (Scott, 1981; Thomas et al., 1982). Some of these, such as the Balearic Isles, Sardinia, southernmost Spain, Italy, Crete, and Romania, show various stages of transfer from incipient to complete (Adrover & Hugueney, 1975; Burchfiel, 1976; Leinders & Meulenkamp, 1978; Vandenberg, 1979; Cohen, 1980).

Effects of Time on Noah's Arks

A problem with invoking small, far-traveled tectonic blocks to explain transoceanic similarities or apparently embedded endemics is that

such travel in oceanic isolation takes a long time, during which significant morphologic changes may have occurred in the passively transported biota. If one accepts that a special taxonomic similarity between transoceanic sister species, genera, or families indicates former continuity of two widely separated occurrences, and one finds that fragments of a once continuous landmass upon which the ancestors of these taxa once existed are now allochthonously embedded in distant continents (Nelson, 1981), then any such taxon must independently be expected on *generally* parsimonious grounds to have existed at the time of the original fragmentation. In the case of "Pacifica" or in arguments about differential Earth expansion, this time can amount to more than a hundred million years, depending on the rate of ocean floor spreading and the distances travelled. Although it is generally recognized that the fossil record is imperfect, it is not likely that the fossil record is perverse, as some cladists would apparently have it. Thus the chances that, say, 15 discerptible sequential character states of horse evolution lasting a million years apiece actually took place in the same sequence but 15 million years earlier in each case, without leaving a record until appearing in exactly the same sequence later, unchanged, I would think to be on the order of e^{-225}, effectively equal to zero. Nor is the amphi-Pacific distribution of human populations likely to be explained by the fragmentation of "Pacifica" as is adumbrated by Nelson and Platnick (1981: 542)! Parsimony is a factor in all science, not just in the preparation of cladograms. With regard to vertebrates, I would think that only rather high-rank taxa, such as a class or subclass, might be involved (if at all) in the "Pacifica" or differential expansion scenarios. But I know of no convincing evidence that any terrestrial vertebrate lineage has been brought alive to the shores of North America from the other side of the Pacific on a fragment of "Pacifica." This is not to say that far-traveled and once submerged tectonic blocks, once they become imbedded in a new land, cannot be further transported along the edges of continents by transcurrent faulting, etc., carrying ancient fossils and newly acquired terrestrial biotas along with them to new destinations.

Planetary Popcorn?

That the Earth has expanded is an idea that can be traced with certainty back to the works of W. L. Green in the nineteenth century (Jordan, 1966, 1971; Carozzi, 1970; Carey, 1976). Modern metaphysical underpinnings for a form of expansion have been provided by Dirac (Wesson, 1973: Davies, 1982) although several investigators have arrived at the concept from empirical studies alone, without knowledge of Dirac's work. Possibly several different expansion mechanisms might work in concert, but appeals to unknown mechanisms should be entertained only when all else fails, as was the case in the early days of continental drift theory.

Dirac (1937, 1938, 1974) concluded inductively that there must be some connection between the gravitational "constant" and time. He, and other students since then, concluded on the basis of his "large numbers hypothesis" that the gravitational "constant" must be weakening, proportional to time elapsed since the Universe began, which Dirac believed to have been about 2 billion years. Current estimates of the age of the Universe are up to an order of magnitude greater and vary, depending on differing determinations of the Hubble constant, from at least about 10 to as much as 18 billion years (de Vaucouleurs, 1982). This gives the postulated expansion process a longer time in which to operate than Dirac originally contemplated, drastically reducing the Phanerozoic component of whatever total expansion might have occurred. That the Earth itself should have participated in Hubble expansion seems reasonable enough. Therefore, since mid-Paleozoic time, say 350 Ma, a maximum of about three percent of the Earth's expansion would have taken place. This amount is smaller than the figure given by Carey (1975, 1976), partly because his value for the age of the Universe was only about a third or a quarter of that now accepted and partly because Carey believed that the expansion accelerated exponentially with time. Owen (1976, 1981, 1983), on supposed empirical grounds that do not take into account the effects of propagating rifts, believes that the Earth's diameter has expanded by 20 percent of its modern diameter since 180–200 Ma. Steiner (1977) also believed in rapid expansion, concluding that the Earth has expanded about 11 percent since Jurassic time, an argument that precipitated a series of outcries and explanations in the June, 1978 issue of *Geology* (e.g., Kaula, 1978).

Vink (1982) and Courtillot (1982) provided models of continental rifting that effectively explain the spherical triangular apparent gores that

are the raison d'etre of attempts to match coasts or continental slopes on an Earth of smaller radius than the present one. As a rift begins to invade a continent, breaking it apart into two continents, the resulting new coasts progressively dilate and also bend down as the rift propagates. Hence the apparent gores.

Actually, what is required is not an explanation of Earth expansion. Expansion may have occurred, but, if the whole Earth expanded uniformly, then there would be no crustal separations to explain and paleomagnetic inclinations would not be expected to change. However, the Earth is not like a balloon in which the contained matter expands and the balloon itself does not. What a balloon does is to deform, thinning to the point of breakage. If a balloon truly expanded, its rubber would thicken instead of thinning as its area increased. If paleomagnetic studies were to be conducted on such a deformed, balloon-like crust, they would show modified field inclination vectors for one of two reasons. Either general crustal thinning would do the job or decrease in curvature would provide a similar result in case the continental fragments did not expand, more or less analogous to the fate of pieces of paper attached to the surface of the balloon. What is needed is an explanation of why, if general expansion has occurred and continents have separated, continental crust should not also have participated in the expansion process affecting the whole Earth, thickening as well as increasing in area. Non-expansion of part of or all of the continental crust thus is an ad hoc assumption in most scenarios. I have seen little quantitative discussion of this in the expansionist literature except that of McVittie (1969), who came to no conclusion other than that different parts of the Earth and other celestial bodies might possibly expand at differing rates at different depths. Usually, the problem is not mentioned at all.

However, if one gives proponents of substantial differential expansion the benefit of the doubt and assumes that only the Earth's core and simatic crust expanded and, as a further ad hoc assumption, that all expansion occurred between the eastern and Western shores of the Pacific, then a maximum of about 1,200 km of separation there due to differential expansion would have occurred since the mid-Paleozoic, when marine faunal similarities between Australia and North America began to drop sharply (Gill, 1958). That differential expansion was, if it occurred, less than 1,200 km or was offset by other factors is indicated by the calculations of McElhinny et al. (1978), who concluded on the basis of paleomagnetic evidence from presumably non-expanding continents that the Earth has had a diameter within one percent of its present diameter since at least the Devonian. McElhinny and his co-workers also concluded that Mars, Mercury, and the Moon have not expanded significantly since Precambrian time. Golombek and McGill (1983) obtain similar results for the Moon.

In any case, on Earth the amount of allowed separation due to differential expansion alone would be a small fraction of the present width of the Pacific Ocean. Thus we may conclude on quantitative grounds that differential expansion, even if it were true, would not help much in the field of paleobiogeography except to increase the degree of some ancient separations by a small amount. Far more important is the fact that the floor of the Pacific is decoupled from its surrounding continents and the size of the Pacific Ocean itself has been shrinking, not expanding, since the time of the Pangaea assembly. Sea floor created is eventually subducted. An area of the ocean floor equivalent to that of the present Pacific Basin has been subducted since early Cretaceous time alone (Larson & Pitman, 1972), and there is ample evidence that the process was ongoing long before that. Such processes have been recycling sediments derived from the continents into the mantle since Precambrian time (DePaolo, 1983).

Recently, however, Nelson and some other students of vicariance biogeography have been impressed by non-quantitatively assessed accelerated expanding Earth models, evidently as a means of explaining amphipacific organismic distributions without recourse to dispersal or to vicariance dependent on currently accepted plate tectonic reconstructions (Nelson, 1981; Nelson & Platnick, 1981). As did Hilgenberg (1933), Halm (1935), Brosske (1962; see Jordan, 1971), Barnett (1962), and Meservey (1969), they obtain a direct route across the Pacific (Panthalassa) by simply removing the Pacific Basin, juxtaposing its sides by postulating a much smaller former Earth on which the continents somehow retained the same area as now, covering essentially the whole surface of the Earth. This superficially attractive solution does not adequately address several questions: 1) where and how deep the ocean water of the world was previously, 2) what is to be done with abundant geological evidence

that an ocean has existed in the Pacific area, for instance off North America's west coast, since the early Paleozoic or Precambrian (Roberts, 1972; Cook & Taylor, 1975; Badham, 1978, 1979; Hoffman, 1979), 3) how 304–311 million year old ophiolites in California (Saleeby, 1982) or Ordovician ophiolites further north (Churkin & Eberlein, 1977) are to be explained, or 4) how evidence of pre-Pangaean Wilson cycles like that of the Iapetus Ocean are to be discounted (Glikson, 1972)? Such an Earth would necessarily have expanded differentially at a much greater rate than is required by Dirac's inductive insights, more or less like a piece of cosmic popcorn. If caused by Dirac's mechanism, however, the expansion envisioned would clearly be evidence that the Universe is much younger than the current consensus would have it. Thus, one might conclude that, if proponents of accelerating expansion are correct, all physics should adjust itself in some major way to their requirements (Kaula, 1978; Steiner, 1978).

But, perhaps supporters of the supposed biogeographical explanatory power of the differential expanding Earth hypothesis have erred in not going far enough. Generalized tracks (Croizat et al., 1974) are drawn between landmasses in such a way as to occupy the shortest distance between them. So the most direct route from Australia to the Americas is actually *through* the Earth, not along its surface. Such a tunnel would do less violence to the models of hopelessly complacent physicists and geologists than would an accelerated expanding Earth model in which, in terms of the model, continents are gratuitously assumed to have remained of fixed area and thickness. If students of transoceanic Pacific vicariance are willing to stretch generalized tracks so that they fall on the Earth's surface rather than within the Earth, why are they unwilling to stretch the tracks so that they go around the Pacific rather than through it?

Against a backdrop of general parsimony and in the absence of a quantitative expansion model, I cannot take the accelerated expanding Earth model seriously as a source of discernible late Phanerozoic biogeographical pattern. For such purposes, either linear or accelerated expansion has been investigated and has been found wanting. Those who disagree should seek a flaw in the arguments presented by Van Andel and Hospers (1969). McElhinny (1973), McElhinny et al. (1978), and Golombek and McGill (1983). Carey (1975) has done so with regard to the arguments of Van Andel and Hospers, but, insofar as I know, McElhinny's work has not yet been seriously challenged, even by Owen (1981, 1983).

Impacts of Apollo-Class Asteroids and Comets

Recently, the possible effects of impacts with the Earth of Apollo-class asteroids and comets have been much discussed (e.g., Napier & Clube, 1979; Emiliani, 1980; Alvarez, 1982; Alvarez et al., 1982; Clube & Napier, 1982). Although such impacts are well correlated with extinctions of calcareous marine microplankton, there is as yet no convincing evidence that these events always correlate with major terrestrial turn-over. At the Cretaceous-Tertiary boundary the effect of an Apollo-class bolide on large terrestrial organisms, such as the last surviving dinosaurs, was apparently nearly synchronous at the power of resolution studied (Russell & Singh, 1978; Russell, 1979; Hickey, 1981; Clemens et al., 1981; Archibald & Clemens, 1982; Archibald et al., 1982; and, especially, Alvarez, 1982, for statistical analysis).

Later, supposedly at 34.6 ± 4.2 Ma (Glass & Crosbie, 1982), another major impact, the cause of the North American tectite strewn field, has been widely discussed. But at 35 Ma there was no especially pronounced terrestrial vertebrate faunal turn-over. Prothero (1982) has noted a minor vertebrate faunal turn-over at 32.4 Ma, but this followed a period of stasis after a major faunal turn-over in the interval from 40 to 37 Ma Keller et al. (1983) give convincing evidence that the North American tectite strewn field occurred at 37.5–38 Ma in the latest Eocene, not later as suggested by fission track age determinations or those based on glauconite. Keller et al. (1983) also found evidence of at least two other tectite strewn fields at about the Eocene/Oligocene boundary, but no mass extinction was associated with any of them.

Recent attempts to correlate the supposed event at about 35 Ma with the Eocene-Oligocene boundary (Glass & Crosbie, 1982) or presumed equivalent boundaries between marine invertebrate or North American mammalian biostratigraphic units have simply ignored abundant high temperature K-Ar dates from volcanic rocks interlayered with fossil bearing sediments whose paleomagnetic stratigraphy can also be studied. These dates calibrate Uintan-Duchesnean-Chadronian faunal and floral turn-over (Leopold & MacGinitie, 1972; Wilson, 1980) in North

America as occurring close to 38 Ma (Berggren et al., 1978) or 36.6 Ma (Berggren et al., 1982; in press). Prothero et al. (1982) come to similar conclusions. Nor could an impact at a later date explain the flood of Asian and/or American arrivals that characterized the Grande Coupure in Europe. In Europe the Grande Coupure has been dated at 37–38 Ma (Gramann et al., 1975; Van Couvering et al., 1981). Iridium-rich layers incorporating undifferentiated Solar System matter are indeed associated with some (but not all) large Cenozoic impacts, but if one hypothesizes that large-scale effects on terrestrial biotas have occurred through the agency of a particular bolide, one should provide clear evidence of simultaneity. This has not yet been produced. Meteoric dust has of course long been known to be a component of the Earth's sediments (e.g., Skolnick, 1959). Moreover, more biological evidence than the extinction of five species of radiolarians (Glass & Crosbie, 1982; Ganapathy, 1982) needs to be associated with the supposed 35 Ma single event if it is deemed to be especially important. Radiolaria were little affected by the impact that occurred in close association with the Cretaceous-Tertiary boundary (Emiliani et al., 1981), so it is unclear whether a causal relation exists. Microtectites and iridium anomalies should be sought throughout the geologic column before those few that are known now are specifically assigned far-reaching importance as evidence of extraterrestrial impacts of sufficient magnitude to have served as forcing factors in the biological world. Already, there appear to be several candidates among the various known large terrestrial impact craters (Hughes, 1979) to be the sources of at least three different Late Eocene and/or Oligocene strewn fields of tectites (Bottomly et al., 1979; Keller et al., 1983). It is equally clear from Hughes's (1979) map that many unrecognized impact structures remain to be found in non-subducted ocean floor. How many more have been lost to subduction is unknown.

Effects of Radioisotopic Calibration on Temporal Distribution

Most of this essay has been concerned with spatial distribution, but recent discussions of rates of extinction and of faunal turn-over (Flessa, 1975; Raup & Marshall, 1980; and other articles on the same general subject in the journal *Paleobiology*) prompt a few brief comments about the obvious but nevertheless seem necessary. A first point is that compilations should be based on specific lineages, not on higher taxa. Technically, it is not genera, families, orders, etc., that originate, evolve, or become extinct. For example, it is the perishing of the last species of a higher taxon that causes the higher taxon to perish. Discussions of the sudden extinctions of higher taxa may well mask a series of more gradual extinctions of various genetically isolated lineages within any particular higher taxon. Studies of extinction, to be convincing, need to discuss the relative abundance and presence or absence of taxa at the species level and to relate this information to measured stratigraphic sections studied in the field rather than to derive their basic information from popular texts such as Romer's (1966) Vertebrate Paleontology.

A related point has to do with rates of faunal change. For these to be calculated, some form of temporal calibration is required, of which the most effective one is a time scale measured in years. Such a calibrated time scale is not yet available for much of the fossil record, at least not at the power of resolution necessary for detailed study. What generally happens instead is that biostratigraphically-based time divisions within a particular interval are treated as aliquots (Fig. 1). The abundance of taxa within these units is assumed to be meaningful, but instead the diversity of a longer interval could be caused by mixing the diversity of two or more unrecognized levels within the unit. This has been demonstrated, for example, in the case of the long North American Wasatchian and Uintan Land Mammal ages relative to the much shorter Bridgerian Land Mammal Age (Berggren et al., 1978). The apparently high diversity of some units given aliquot status in biostratigraphy may be caused simply by their long duration and therefore by their temporally composite sampling of the passing kaleidoscope of life (Raup & Marshall, 1980) (Fig. 2).

Extensions of Simpson's Biogeographic Principles

Simpson (1940a, 1940b, 1943, 1952, 1953, 1965) developed the notions of biogeographic corridors, filters, and sweepstakes (McKenna, 1975). Basically, these constitute a spectrum of permissiveness with regard to dispersal and possess statistical signatures when sampled in the geological record. Provided the record is adequate, one should in principle be able to recog-

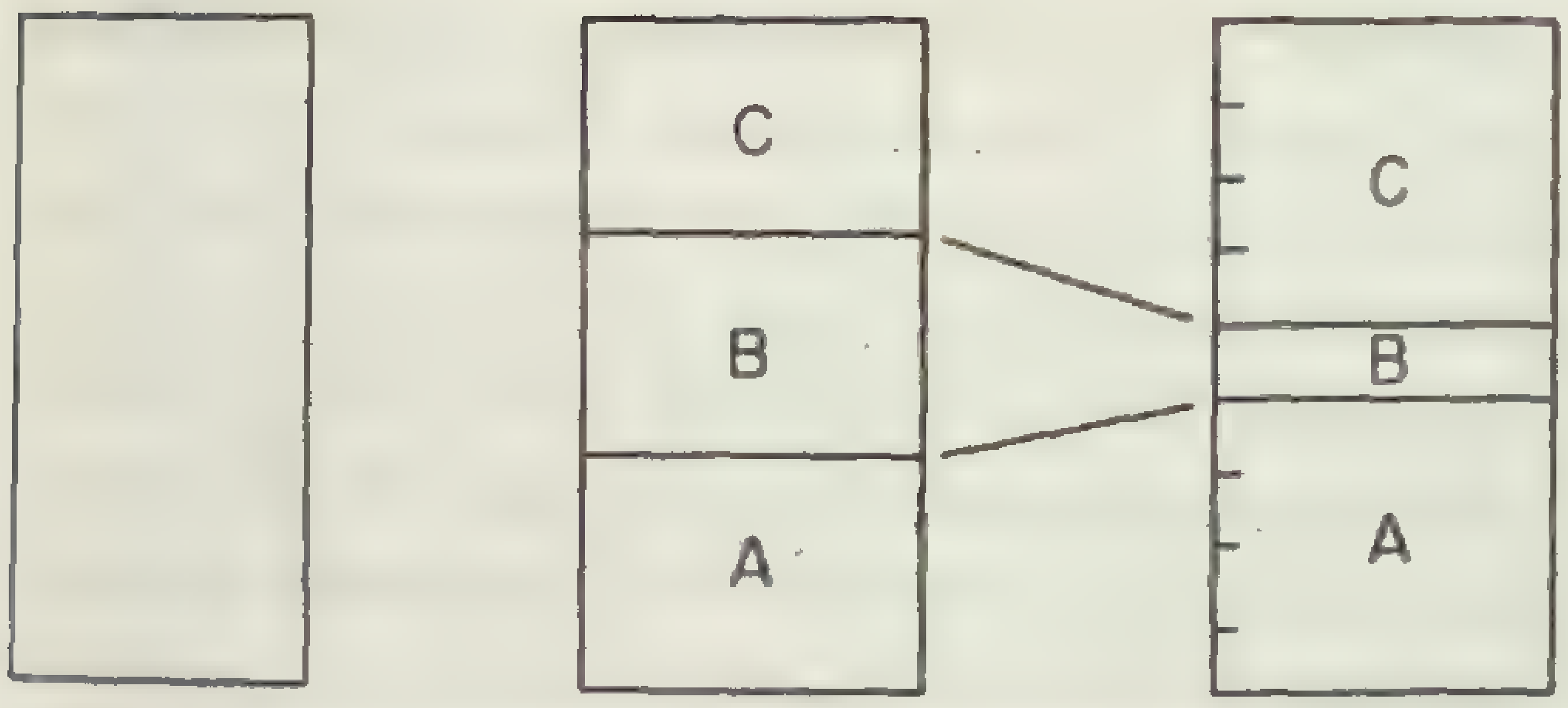

FIGURE 1. As biostratigraphic units are recognized, they tend to be given aliquot status. Although their temporal sequence is known, the temporal duration of units A, B, and C is not at first known but is later calibrated.

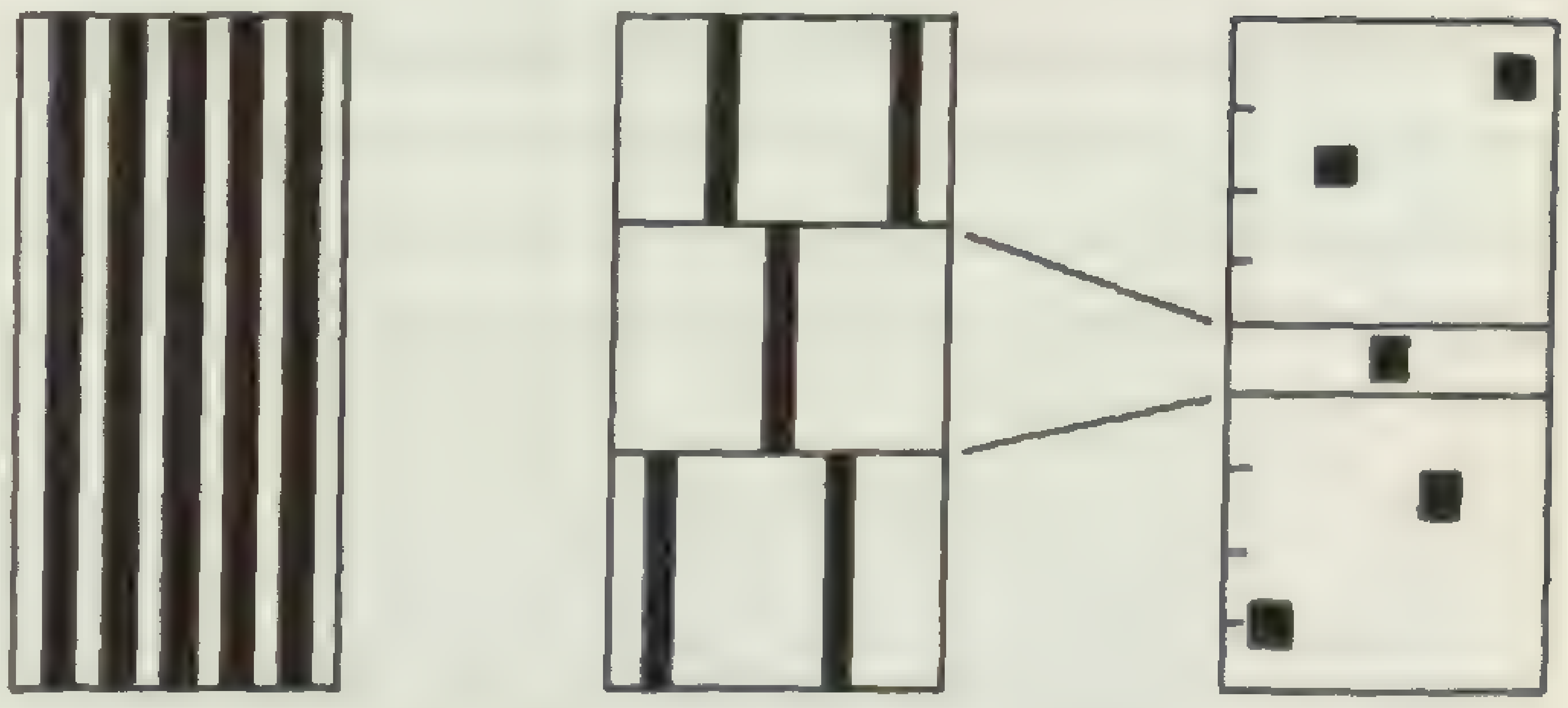

FIGURE 2. Before biostratigraphic subdivision, the biological diversity of a sequence of rocks is merely known to occur in the sequence (left). Upon biostratigraphic subdivision into aliquot parts, the diversity of known fossils within the aliquots can be compared and may be found to differ (center), leading to estimates of rates and intensity of various evolutionary phenomena. When the duration of the biostratigraphic subdivisions is provided by temporal calibration (right), the apparent diversity of units of long duration may turn out to be better interpreted as the result of mixture of sequential diversities that are themselves relatively constant. Previous estimates of the evolutionary processes involved may turn out to have been in error.

nize when two areas were connected to each other by a continuously habitable substrate, when the substrate was partially a barrier, and when the barrier was more complete as in the case of random over-water transport of organisms to islands. Assuming the imperfect geological record of organisms to stop short of perversity, one can assess the extinct biotas of various landmasses of the Earth and make reasonable estimates from biological resemblances whether certain land areas were freely accessible to each other's biotas. Simpson based his arguments on the stable-continent rationale and most of his examples are drawn from fossil mammals. However, his principles are adaptable to a mobilistic world and are still valuable in spite of criticism of past excesses by Du Toit (1944), and in spite of simple avoidance of discussion of them by most vicariance biogeographers.

There is no need to repeat all of Simpson's arguments here, but suffice it to say that terrestrial corridors are defined when biological resemblances between two distant samples are approximately the same as would be found at present between samples drawn from opposite sides of a continent, say Eurasia or North America. If a corridor came suddenly into existence, dispersal would be in both directions and would not be long delayed. Ecologically balanced biotas would be involved. At the other end of the spectrum, sweepstakes dispersal would be characterized by random arrivals, one-way transfers, ecological imbalance, and delayed introductions. In between would be various types of filters that permitted some but not all organisms to pass. Simpson discussed this spectrum as though its components represented separate processes, but in a mobile world it is especially obvious, for instance, that whole oceans were once inches, then feet, then miles wide. At certain points in this progression the statistical properties of Simpson's corridors, filters, and sweepstakes would each have helped to shape the evolutionary history of the biotas involved.

Because of the stabilist rationale implicit in Simpson's earlier work, Simpson believed one-way transfers of balanced biotas to be unlikely. To be fair, it should be noted that Simpson did toy with the idea of one-way or "revolving-door" transfer by means of sequentially uplifted and then subsided blocks, thus avoiding large-scale horizontal displacements such as those contemplated in present geological thought. However, under a mobile rationale such transfers are possible passively, as the result of motions of parts of landmasses to join others. As have many others, I have elsewhere (McKenna, 1975) called the substrates on which such one-way transfers take place "Noah's arks." A related concept dealing with fossils is that of "grounded Viking funeral ships" (McKenna, 1975). The idea here is that fossils, as well as living organisms, can be carried by moving crust and added to other landmasses by the process of continental accretion, as has been demonstrated for North America's west coast (Jones et al., 1978). The difference is that the fossils that come to be imbedded in a new host landmass do not stray from their resting places to infect the rest of the landmass's biota. Like transferred fender paint in an automobile collision, they reflect only former allegiances.

Such transfers are to be expected as the result of multiple Wilson cycles that open and close oceans and, on a smaller scale, along large transcurrent faults that cross water barriers.

VOYAGES TO NOWHERE AND RETURN

Another feature of mobilistic tectonics that permits some additional embroidery of the theme that plate tectonics supplies mechanisms undreamed of in stabilists' philosophy is the phenomenon of back-arc spreading. This results in the separation of an intracontinental volcanic chain, such as the Andes or Cascades, to become an offshore arc that may later be driven back against the same continent from which it originally separated. Japan is undergoing this process (Uyeda & Miyashiro, 1974), and a similar process affected the southern Andes in the past (Dalziel et al., 1974; Dalziel & Palmer, 1979). Such separations occur because the cooling of sinking slabs of oceanic crust sometimes results in seaward jumps of subduction zones. This is because, in effect, the whole slab sometimes pulls away from the surface at a point closer to its generating ridge than the point of its earlier subduction. The volcanic arc behind the subduction zone therefore moves offshore. Continued subduction under an advancing continent would result in the arc's rejoining the continent unless another seaward jump of the subduction zone occurred in time (Uyeda, 1981). During the time that such an island arc was in isolation, both vicariance and dispersal followed by differentiation would produce peripheral isolates in abundance. Then these would be merged with the biota of the mainland. Much diversity could be created in this manner, but there could be a substantial time delay before re-introduction to the mainland.

Voyages to nowhere and return are not the result of simple intermittent barrier erection and destruction such as might be envisioned in the case of coastal islands created by eustatic rises of sea level, followed by a fall. They involve passive separation and physical removal of a biota to a significant distance on a moving substrate, followed by return and passive merger.

ESCALATOR COUNTERFLOW

Everyone has seen children turn escalators into treadmills by walking counter to the expected flow of traffic. As long as the child walks at the same speed that the escalator maintains in the opposite direction, the child remains stationary with regard to the escalator's foundations. What does this have to do with biogeography? Consider Iceland.

Iceland lies at the north end of the Atlantic Ocean, astride the Mid-Atlantic Ridge. It is a volcanic edifice built above a hotspot that has produced abnormally large volumes of lavas episodically and variably throughout most of the Cenozoic (Schilling et al., 1982). The oldest rocks on Iceland are known from coastal areas in the eastern and northwestern parts of the island, where they are about 16 million years old (Moorbath et al., 1968). Fossil plants and insects are known from late Tertiary volcaniclastics in northwestern Iceland, but as yet no fossil mammals have come to light. Geologically, Iceland is a steady-state phenomenon, in that its land spreads from the center above the hotspot and sinks below sea level after about 15 or 20 million years of lateral transport. Thus the main subaerial part of the Icelandic lava pile has covered more or less the same area of crust for a long time (Vogt, 1972). Early in the Cenozoic, early Iceland rose up to choke the whole North Atlantic for a time, creating a land bridge from Greenland to Scotland. Later, as the North Atlantic widened, Iceland came to be partly and then wholly isolated.

Apparently, Iceland retained its connection with Greenland and thence to North America longer than it did with Scotland (Friedrich, 1966; Grønlie, 1979). In the Miocene, Iceland still supported species of *Magnolia, Liriodendron, Juglans, Betula, Acer, Abies, Ulmus, Sequoiadendron, Sassafras, Populus,* and *Picea,* as well as a species of the hickory aphid *Longistigma* (Heie & Friedrich, 1971). Their respective closest species-level relatives at the time were in North America rather than in Europe (Friedrich & Símonarson, 1981). It is not yet known when these organisms *first arrived* in Iceland. At present, however, after the glacial events of the Pleistocene and subsequent repopulation of most of the flora by various means, Iceland's flora is primarily European in character (Einarsson, 1963).

New subaerial crust has been more or less constantly created at the generating plate boundary that crosses central Iceland, separating the growing Eurasian and North American plates. Because the Icelandic hotspot is associated with the plate boundary and because abnormally large volumes of volcanic products are brought to the

surface, Iceland is subaerial rather than just another part of the Mid-Atlantic Ridge. About 20 million years after any particular batch of new crust is created at the plate boundary over the hotspot, the crust will have been moved aside because of the creation of still newer crust at the boundary, eroding at the surface and cooling and subsiding to sea level and below as it spreads at a rate of about one centimeter per year. After sinking beneath the waves, 20 million year old or older Icelandic volcanics on either side of Iceland simply become parts of the submarine Greenland-Scotland Ridge.

The land surface of Iceland at any particular time thus comprises two "down" escalators arranged back to back, whose oppositely directed lateral components of motion start at the plate boundary in the middle and continue to the ocean on opposite coasts. To have escaped drowning, the terrestrial biota of Iceland merely needs to have moved over the land surface toward Iceland's central volcanic zone at a rate of about one centimeter per year for as long as the hotspot has maintained Iceland as an island above sea level (Fig. 3). Subaerial Iceland began to form at about the time of marine magnetic anomaly 24, at about 54 Ma, and appears to have remained connected to Greenland until some time in the Miocene. It might therefore be expected that Iceland once possessed a biota (prior to its being almost entirely snuffed out by glaciation) whose origin from a continent could have been, except for later dispersals, earlier than the oldest rock now present above sea level in Iceland (McKenna, 1983). Twenty million years from now, after Iceland's present rocks have moved beneath the Atlantic, some of the members of the present Icelandic biota may still be there on Iceland's newest crust, slowly climbing up "down" escalators.

Thus, it is permissible to generalize that steady-state islands lying over volanic spreading centers can have biotic components that are significantly older than the oldest rocks now present either at the island's surface or located directly underneath. Such ancient terrestrial components can have been continuously in residence on dry land for a length of time that need not necessarily be limited by the age of the oldest known insular rocks but may instead date back to the beginning of hotspot activity. An important way to test such a possibility would be to compare the hotspot age with the known geologic ranges of closely related sister taxa occurring elsewhere in the world. Obviously, taxa in passive isolation on evolving hotspots must be as old as the hotspot's isolation or must have arrived by dispersal at some later date.

Hopscotch on the Escalator

A potential mode of distribution that is in some ways intermediate between vicariance and dispersal is apparently represented well by the Hawaiian Islands and perhaps by other mid-plate hotspot edifices (Axelrod, 1972).

Vicariance, it will be remembered, results when a barrier arises *after* a distribution of organisms has been established, breaking it apart into isolated sister taxa (Croizat et al., 1974: 277–278; Nelson & Platnick, 1981). One way, but certainly not the only way, to cause vicariance is to pull apart the passive riders on two differentially moving tectonic plates. Dispersal, on the other hand, crosses *pre-existing* barriers to establish a new, expanded distribution, but processes such as the founder effect and difficulties of passing through the same barrier in the opposite direction (if, say, oceanic currents are involved) allow differentiation of sister taxa after dispersal occurs. Further, dispersal is an active process whereas vicariance brought about by tectonic plate motions does not require movement above the substrate on the part of the participants. Both processes may be responsible for the origin of biotas, particularly those of islands.

The Hawaiian Islands are collectively a long term steady state phenomenon, like Iceland, but, in contrast to the latter, the Hawaiian chain is not located on a mid-oceanic ridge nor has it recently been connected to any continental mass (Jackson et al., 1972; Dalrymple et al., 1973; Dalrymple et al., 1981). Both places are the result of subaerially produced hotspot lavas; but in the case of the Hawaiian chain, the Pacific Plate, which currently underlies the chain, is moving with respect to the hotspot and thus carries away the volcanic piles generated by the hotspot. The hotspot itself has moved relatively little, if at all, with respect to Earth's spin axis since Cretaceous time (Hammond et al., 1979; Suarez & Molnar, 1980; Gordon & Cape, 1981). At present the sea floor of the Pacific Plate in the Hawaiian area is moving west-northwestward over the Hawaiian hotspot, passing it by (Wilson, 1963) and carrying formerly tropical islands northwestward into cooler waters (Greene et al., 1978). How-

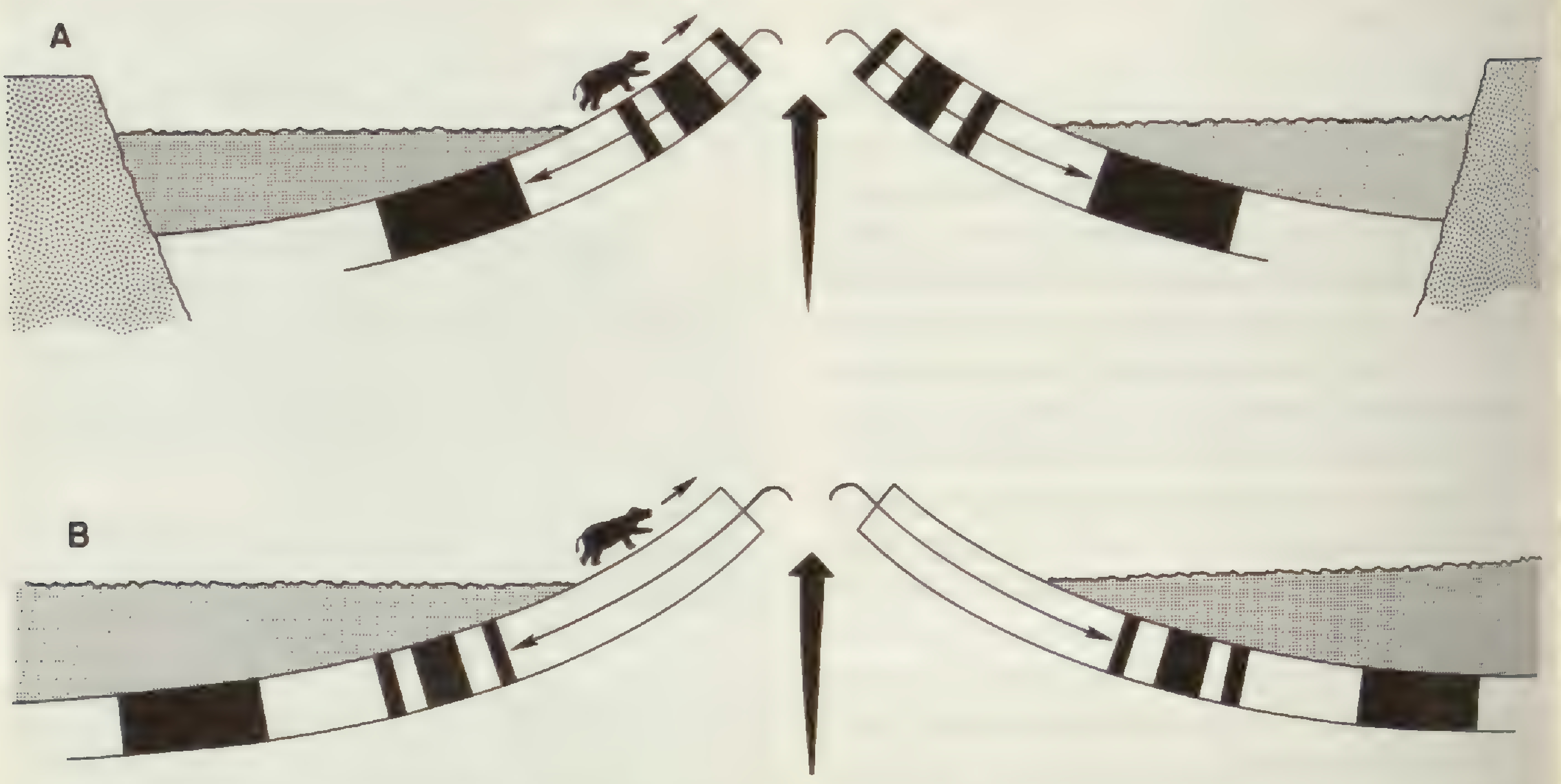

FIGURE 3. Escalator Counterflow. This cartoon attempts to show two stages in the geologic history of a mid-ocean ridge volcanic island such as Iceland. A: New crust rises from the underlying hotspot and spreads in opposite directions from the plate boundary. Magnetic polarity reversals are recorded in the volcanics as they solidify, resulting in a recognizable pattern that is symmetrical with regard to the plate boundary. Separating continents are still nearby, but the island is now surrounded by deep water, whereas it once choked the incipient ocean between them when sea-floor spreading had just begun. To avoid a salt water bath, the island's biota must move toward the plate boundary at the same rate that new crust is created—perhaps a centimeter or a few centimeters per year. B: After some time (shown by the retreat of the recognizable magnetic polarity pattern), the island is still there, although composed of younger crust. The separating continents are now no longer near, but the biota could still be present, evolving in isolation and being winnowed by extinction as well as added to by occasional arrivals from elsewhere. Thus, it is possible that some island biotas either have or have had composite mixtures of lineages that arrived both by dry land and by the various agencies of transoceanic dispersal.

ever, the rising magma column is not constantly beneath a weak plate boundary as is the case with Iceland. Rather, the column must bend as the plate passes overhead, occasionally breaking and reestablishing a more direct route to the surface. Every so often magma breaks through the plate from below to form new volcanoes above, but these form generally at the southeast end of the Hawaiian chain, first as submarine volcanoes (Emery, 1955) and then massive subaerially projecting structures as they grow in size. Indeed, one is forming beneath the surface of the ocean at present, southeast of the Island of Hawaii at Loihi Submarine Volcano (Klein, 1982; Malahoff et al., 1982). Some of the individual volcanoes in the Hawaiian chain reach a height of 9,000 meters above the sea floor, projecting up to about 5,000 meters above sea level. Meanwhile, the crust to the west-northwest cools as it departs the vicinity of the hotspot. Gradually it sinks and the older volcanic piles lying on it erode (Fig. 4). Eventually they sink beneath sea level (Vogt & Ostenso, 1967). The oldest islands of the Hawaiian chain are therefore located in the west-northwest, as J. D. Dana realized as early as 1849 and as was finally demonstrated by potassium-argon dating more than a hundred years later (McDougall, 1964). Several volcanic piles in the chain may have been present on the Pacific Plate before their sites passed over the hotspot, however. Wentworth Seamount and Necker Island have yielded Cretaceous K-Ar ages (Clague, 1975). Rotondo et al. (1981) have discussed the possible biological consequences of adding these edifices to the Hawaiian chain.

The sporadic nature of the hotspot vulcanism results in gaps between the islands, but these are not very great in most cases. Islands that are initially separate may join as the volcanic piles enlarge. The combined Hawaiian-Emperor chain contains 107 or more recognized volcanoes (Bargar & Jackson, 1974).

The Hawaiian process has been going on like this for a very long time. About 43 million years ago the present WNW motion of the Pacific Plate began (Dalrymple et al., 1977; age corrected for currently accepted decay and abundance constants). During the early Cenozoic the motion of

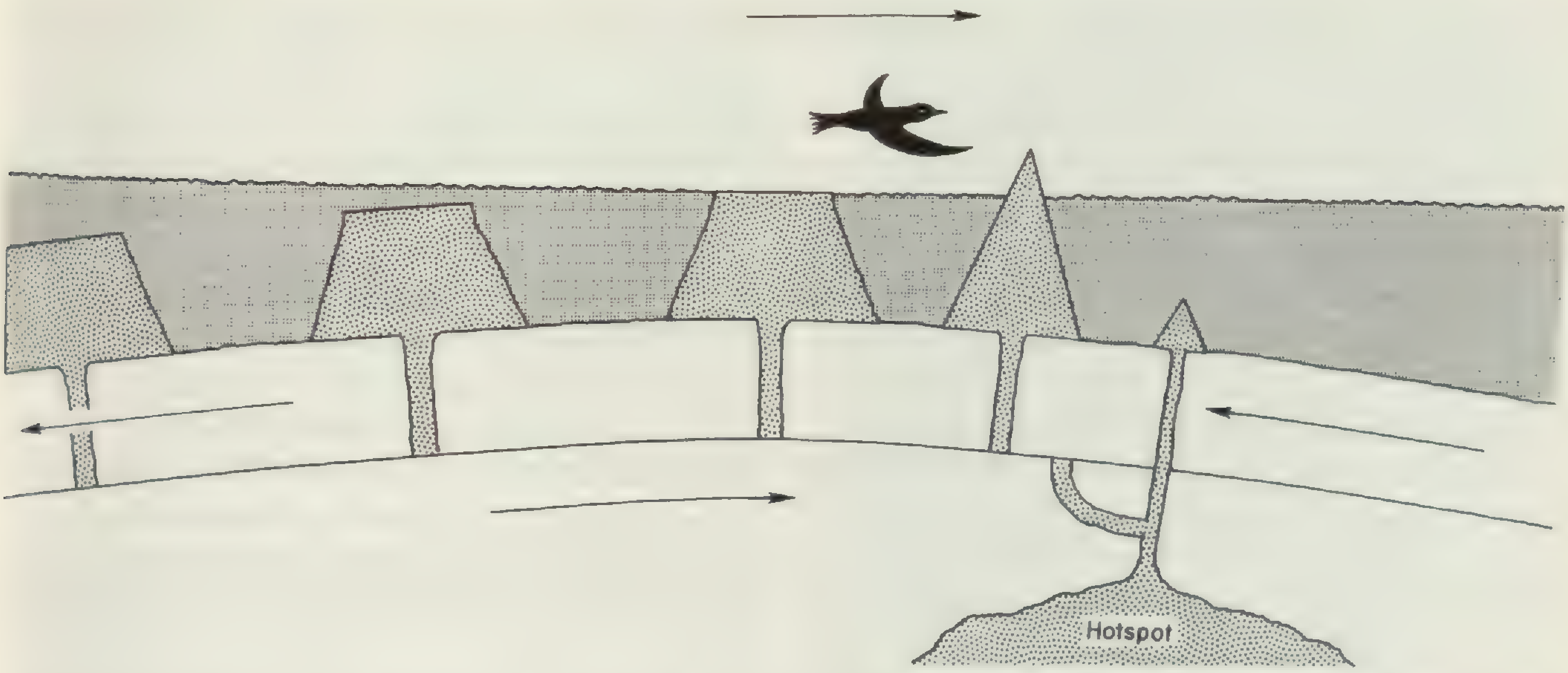

FIGURE 4. Hopscotch on the Escalator. Based on the model provided by the Hawaiian Islands, it is possible to envision a situation in which new islands arise at one end of an island chain while others sink at the other end. Some new islands would coalesce, but others would be separated by short water gaps. This process could go on for a very long time and islands (not necessarily the same islands) would have been continuously present during that time. Rocks on any particular island now above sea level would be very young, but that would not mean that the biota of the islands had necessarily arrived in the islands recently or that all members of the biota would have had to cross whatever oceanic barriers now isolate the islands from other landmasses. Dispersals among and to the ongoing sequence of islands could have occurred over a very long time and truly ancient inhabitants might be present that had never had to cross more than minor water barriers in order to be present on at least one island at any particular time. If the hotspot were old enough, it would probably once have been beneath a continent. Thus some terrestrial endemics might have arrived across barriers less stringent than those usually postulated in the biogeographical literature.

the western part of what is now the Pacific Plate (Izanagi Plate of Woods & Davies, 1982) was more nearly northward because of the action of the Emperor Spreading System, but prior to about 67 Ma. Pacific Plate motion was also west-northwestward (Farrar & Dixon, 1981; but see Gordon, 1982). The trace of the Hawaiian hotspot on the present-day Pacific Plate turns northward at Yuryaku Seamount (Long. 172°E, Lat. 33°N), where it continues as the Emperor Seamount chain (Morgan, 1972). Basalt dredged from Yuryaku Seamount has an age of about 43 Ma (Clague et al., 1975; age corrected). One of the most southerly of the drowned volcanoes of the Emperor chain, Koko Seamount, has an Eocene age of about 47 Ma on the basis of K-Ar methods (Clague & Dalrymple, 1973; age corrected) and may be slightly older than that on the basis of nannofossils of the *Discoaster lodoensis* Zone from its sedimentary cap (Moberly & Larson, 1975). The Emperor Seamount chain extends as a string of drowned volcanoes as far as the present edge of the Pacific Plate, where Cretaceous forerunners of Hawaii, now mere guyots, are being consumed in a cusp between the two curved oceanic subduction zones at the Aleutian and Kurile trenches. Meiji Seamount at the north end of the presently available Emperor chain is about to be subducted there. The oldest fossils from sediments on Meiji Seamount (DSDP Site 192) are at least 70 million years old (Scholl et al., 1971) and are of near tropical organisms. By Oligocene time Meiji had moved north far enough to encounter subarctic conditions (Scholl & Creager, 1973). How long before the beginning of the Cenozoic "Hawaiis" older than Meiji Seamount were being created, transported, subsided, and eventually consumed is not known because of the unfortunate habit of subduction zones to obliterate direct evidence. Nevertheless, a large number of previous Hawaiian-Emperor Islands may have been subducted because the consuming arc systems have apparently become choked long enough to form the cusp between the arcs. The Hawaiian hotspot and its fossil trail of mid-oceanic lava piles could even have already been in existence before the beginning of its presence under the Pacific Plate. It is conceivable that truly ancient versions of Hawaii could have formed in contact with or even on top of a continent that happened to be passing over the hotspot.

For this reason, it is possible to envision a constant winnowing process that would result in erratic distributions within the subaerial part of the chain as terrestrial organisms were forced to play the children's game of hopscotch in order to survive. As new islands formed at one end of the chain, others were sinking at the opposite end. Thus, as with Iceland, the terrestrial fauna and flora of the present-day Hawaiian chain may well be derived, not necessarily totally from long-range over-water transport but rather at least in part from an early vicariant event followed by a series of short dispersals (Axelrod, 1960, 1972). The average distance between volcanoes along the Hawaiian chain is about 56 km; in the Emperor chain the average is about 77 km. Such distances would not be difficult for many insects or flowering plants to cross, as for instance appears to be the case in the Solomon Islands (Whitmore, 1973) or near Puerto Rico (Heatwole & Levins, 1972) at present.

Although the rocks of any particular island still above sea level in the present-day Hawaiian chain are very young (Zimmerman, 1948), the ancestors of some of the present inhabitants of the island may have been living in precarious mid-oceanic isolation for more than a hundred million years. Authors steeped in a stable continent rationale, like Zimmerman (1948), Carlquist (1974, 1982), or Carson (1982) were unable to appreciate this mobilist notion. This is because the Hawaiian chain, like Iceland, is the result of steady-state phenomena. As new Hawaiis are created, old ones sink beneath the waves to the northwest of the string of lava piles created by the Hawaiian hotspot on the Pacific Plate as the latter moves northwestward over the hotspot. Thus, arguments for rapid evolution of Hawaiian *Drosophila* (e.g., Carson, 1976; Kaneshiro & Ohta, 1982) may in some cases overestimate evolutionary rates of species origin by as much as two orders of magnitude. The apparently very ancient arrival in the Hawaiian Islands of primitive land snails that so puzzled Pilsbry (1900, 1916) or of those from the lower Miocene of Bikini in the Marshalls (Ladd, 1965) may indeed be real and permitted by the hotspot history of the areas. Even dispersals to the islands from far away could have been taking place over a much longer time span than that represented by the oldest presently exposed rocks of the Hawaiian Islands, thus helping to explain the differentiation of birds like the Hawaiian finches (Hawaiian honeycreepers), various flightless geese, rails, and an ibis, three species of an extinct genus of owls, and still other endemic birds that occur in fossil deposits of Kauai, Oahu, Molokai, and Maui (Olson & James, 1982).

Obviously, the longer the winnowing process went on, the greater would be the probability of extinction of any original vicariant lineages and the more erratic in taxonomic composition would be the remaining sample of original terrestrial immigrants or early dispersals to Hawaii or other hotspot islands. In the Pacific Ocean alone there are many potential examples of the process, such as the Tuamotus and their symmetrically related Nazca Ridge counterpart, the Austral-Cook chain, the Easter-Sala y Gomez chain, the Juan Fernandez seamount chain and Juan Fernandez itself, the Galapagos-Carnegie Ridge area and Cocos Ridge. However, the Line Islands may not have been generated by a hotspot of the Hawaiian-Emperor type (Haggerty et al., 1982). I have argued here, however, that on geological grounds it is by no means mandatory to conclude that all inhabitants of presently isolated hotspot island groups arrived by relatively recent long-distance dispersal over water or necessarily had ancestors that did so. Rather, a series of short dispersals, carried out over a long time, may explain the existence of some of the taxa present. Original terrestrial immigrants and arriving products of over-water dispersal alike would be potential players of hopscotch on their moving substrates from the moment they began residence over a hotspot.

Clearly, in the case of some island groups, the theory of island biogeography as developed by MacArthur and Wilson (1967) is in need of modification. Olson and James (1982) have already noted this with regard to the avifauna of the Hawaiian chain because of the recent realization that the extinct endemic avifauna was more than twice as diverse as the present one. The effect of a winnowing action over a long period of time also needs to be taken into account in future work because winnowing would produce the same results as are generally attributed to the sporadic agencies of long-distance dispersal.

Closing Note of Caution

In this paper I have tried to list some geological processes that might help to explain some biological distributions in space and time. I have tried also to review some extraterrestrial and even cosmological causes that might influence these distributions either directly or indirectly. As a result, I have been led to discount theories of

mean spin axis stability change, the "Pacifica" concept as an explanation of discernible Cenozoic biogeographic pattern, and accelerated differential Earth expansion as a similar explanation. I have also taken the view that "what is good for mammals must be good for everybody," but if the conclusions based here on geology and on mammals are tested and found wanting on the basis of studies of other organisms, then progress will have been made. Inasmuch as the paper was prepared for a botanical symposium, it will be interesting, at least for me, to see if the geological processes discussed here lead to any new insights regarding the floras of various parts of the Earth.

I must caution the reader, however, not to just accept the dictates of plate tectonics in place of analyzing geology and biology separately in order to preserve mutual testability. It is curious how willing some biologists are to believe the geologists, yet there is a far smaller flow of information in the opposite direction. Few geologic papers cite biological attempts to work out paleogeography, although Wegener did not hesitate to do so. Probably this is because the efforts of the biologists have not seemed to be very rigorous or quantitative to geologists and geophysicists. Mammalogists, geologists, and, yes, the botanists, need to analyze their data by means of the cladistic methods developed recently by vicariance biogeographers and also by the more classical and statistical methods of Simpson, the latter stripped of their stabilist shortcomings and amplified by the addition of some new effects generated by mobilist geology. There are dangers of circularity and non-testability if one incorporates data too early that should first be used as tests, but, once that phase is completed, synthesis is in order.

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NOTE ADDED IN PROOF: While this paper was in press, the book *The Expanding Earth, A Symposium* (Symposia of the Geology Department, University of Tazmania, no. 6, 1981, 213 pp.) was brought to my attention. The Symposium contains 54 articles, many of them strongly in favor of earth expansion of one sort or another and opposed to large-scale subduction. I do not find the arguments presented in these papers convincing, and therefore see no reason to modify statements made above. In a quantitative contribution to the Symposium, A. D. Stewart strongly bolsters the conclusions of McElhinny, Taylor, and Stevenson (1978) that the Earth has not changed appreciably in radius since the Paleozoic.

LATE CRETACEOUS AND CENOZOIC VEGETATION IN CHINA, EMPHASIZING THEIR CONNECTIONS WITH NORTH AMERICA[1]

Jen Hsü[2]

Abstract

The close floristic relationship and disjunct occurrence of many plant taxa between eastern Asia and eastern North America has been given special attention by many botanists. Formerly some people thought that this close floristic link was a result of extensive migrations mainly through Beringia, but recently plate tectonic studies demonstrated that the opening of the North Atlantic Ocean was completed as late as the middle Eocene and the land bridge (Beringia) between Asia and North America was not available until the Miocene. Thus the extensive migrations via Beringia did not occur before the Miocene. The present paper reviews the Late Cretaceous and Cenozoic vegetation in China, enumerating plant megafossils of the Late Cretaceous and the Cenozoic Periods so far recorded there. One-half to two-thirds of the Late Cretaceous plants and one-fourth to one-half of the Late Eocene taxa seem similar (or nearly identical) to those of North America, and some plants are cosmopolitan in Laurasia. This indicates that these plants must have migrated directly between eastern Asia and eastern North America via Europe. So far as the megafossils are concerned, after the Eocene only a few Chinese species are common with those of North America. So most of the isolated and disjunct genera of eastern Asia and eastern North America are remnants of ancient plants widely distributed all over the Northern Hemisphere. Eastern Asia and eastern North America at present are two relic temperature centers of the Northern Hemisphere.

The recent flora of China, one of the richest in the world, is a mixture of northern temperate elements and tropical to (northern) subtropical elements. It is characterized by many relic genera and has a close floristic relationship with that of eastern North America.

As to the relicts, in ferns there are *Angiopteris* and *Archangiopteris*; in gymnosperms, *Ginkgo, Metasequoia, Cephalotaxus, Amentotaxus, Torreya, Taxus, Pseudolarix, Tsuga,* and *Pseudotsuga*; and in angiosperms, *Magnolia, Trochodendron, Liriodendron, Saururus, Illicium, Schisandra, Nelumbo, Euptelea, Eucommia, Cercidiphyllum, Aralia, Nyssa,* and *Menispermum.* Most of them are relic genera of the Late Cretaceous.

Fossils like *Ginkgo* and *Angiopteris* have been recorded from southwestern China in the Late Triassic (Hsü et al., 1974); *Torreya* and *Taxus* were described from the Jurassic of Europe by Florin (1958); *Metasequoia* was quite abundant in the Late Cretaceous and the Late Eocene of northeastern China. *Metasequoia, Glyptostrobus, Cryptomeria, Cunninghamia, Cephalotaxus,* and *Amentotaxus* were widely distributed in Eurasia and North America during the Late Cretaceous (Florin, 1963). Now some primitive families of angiosperms, such as, Magnoliaceae, Calycanthaceae, Schisandraceae, Nyssaceae, Staphyleaceae, Platanaceae, Saururaceae, and Illiciaceae are widely distributed both in South, East, Central, and southwestern China on the one hand and eastern North America on the other. The genera *Fagus, Lithocarpus, Castanea, Quercus, Trigonobalanus, Diphylleia, Lindera, Astilbe, Itea, Hamamelis, Cladrastis, Carya, Buckleya, Stylophorum, Penthorum, Decumaria, Gymmocladus, Ascyrum, Halesia, Chionanthus, Campsis,* and *Catalpa* are examples of the distribution pattern between these two regions (Li, 1971). Others like *Wisteria, Apios, Pachysandra, Glaucidium, Gordonia, Nyssa, Chionanthus* s.s., *Stewartia, Panax, Pieris, Lyonia, Epigaea, Shortia, Gelsemium, Veronicastrum, Phryma, Mitchella, Triostreum, Zizania, Diarrhena, Croomia, Symplocarpus, Tipularia, Celastrus,* and *Diospyros* are also disjunct between eastern Asia and eastern North America (Li, 1971, 1972).

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These genera, formerly believed to number about 80, are now increased to more than 120, among which 112 are recorded from China (Wu, 1984).

To these facts special attention has been paid by many phytogeographers since the time of Asa Gray (1846) and later on by Good (1947), Li (1971, 1972), Wu (1984), and many others. The cause of this disjunction has been demonstrated by various authors from paleobotanical, ecological, and floristic points of view. Li (1971: 404–405) thought that "the present isolated and disjunct floras of eastern Asia and eastern North America appear to be the remnants of a great mesophytic forest that extended over all the northern hemisphere and reached the arctic regions in the Tertiary. Geological changes, including mountain elevation, submergence, climatic variations, glaciations, etc., have destroyed and changed the floras of many lands so that this mesophytic forest of the Tertiary in the northern hemisphere survives in eastern Asia and eastern North America, with only relicts scattered in southeastern Europe, western Asia, and western North America." But Li did not mention the route of migration. However, Takhtajan (1969, p. 175) wrote that during the Late Cretaceous there existed extensive migrations and close links between Eurasia and North America, both by the North Atlantic route (across the landbridge that included what is now Greenland and Iceland) and by the North Pacific route (through Beringia). He further suggested that the link through Beringia was a particularly strong one and served as a bridge joining North America directly to eastern Asia. Anyway, judged from current paleomagnetic investigations, there was no land bridge in the Bering area available between Asia and North America before the Miocene.

In the present paper I review the late Cretaceous and Cenozoic history of the vegetation of China, trace the successional stages of the past floras in China, analyze the possible causes for survival of such a large number of relics in China, and discuss the relationship of the Chinese past floras with those of eastern North America, particularly emphasizing the migration routes between eastern Asia and North America.

Geology and Paleogeography

According to the paleogeomagnetic data given by Dietz and Holden (1970) during the late Paleozoic and the early Mesozoic, North America, Greenland, and Eurasia were united together as a supercontinent, Laurasia. Even up to the start of the Tertiary, northern North America remained firmly attached to Eurasia, with Greenland sandwiched between them. Van der Linden (1975) proposed that the Labrador Sea in the North Atlantic opened in two stages, the first in the late Jurassic–early Cretaceous (about 138 to 110 million years ago) and the second in the early Tertiary (about 60 to 47 million years ago). By the Late Cretaceous, southern Europe was situated at a lower latitude somewhere about 15 to 30°N, the eastern United States at 19 to 20°N, and the Bering area at a higher latitude at 75°N (Dietz & Holden, 1970).

Passing on to the start of middle Eocene (about 49 million years ago) North America and Greenland began to separate from Eurasia and the North Atlantic became a major ocean (Raven & Axelrod, 1974; Schuster, 1976). Europe had drifted some degrees northward (Dietz & Holden, 1970).

According to these authors, India was cut free from east Africa and initiated its migration northward at the beginning of the Jurassic (about 180 million years ago). McElhinny (1970) presented data indicating that the initial rifting took place only in the Mid-Cretaceous, about 100 million years ago. So it is safe to say that the Indian block migration started only after the middle Cretaceous. This plate, drifting northward some 5,000 km at an average rate of 7.5 cm per year, with rates varying from 16 cm per year to less than 6 cm per year, reached Eurasia and joined up with northern Xizang (Tibet) by the middle Eocene, about 40 to 45 million years ago, to become a subcontinent of Asia (Hsü, 1978). The suture of the Indian plate and the Eurasian plate lies along the Yarlung-Zambo valleys. So the southern part of Xizang is actually a part of Gondwanaland.

At the same time, the Himalayan orogenic impulses affected by the collision of the Indian plate and the Eurasian plate caused the uplift of the Himalayas and withdrawal of the Tethys, the Obé Sea in Central Asia, and the Kachi Bay in western Sinjiang, during the time of Oligocene (about 25 to 40 million years ago).

By the estimate of Deffeyes (1973), the tectonic movement of the Pacific plate was northwest until 60 million years ago. Until 25 million years ago, the plate moved directly northward. Up to the present it moved 1,500 km at an average rate of 25 cm per year. Today, for certain plates, migration rates of 16 cm per year are generally ac-

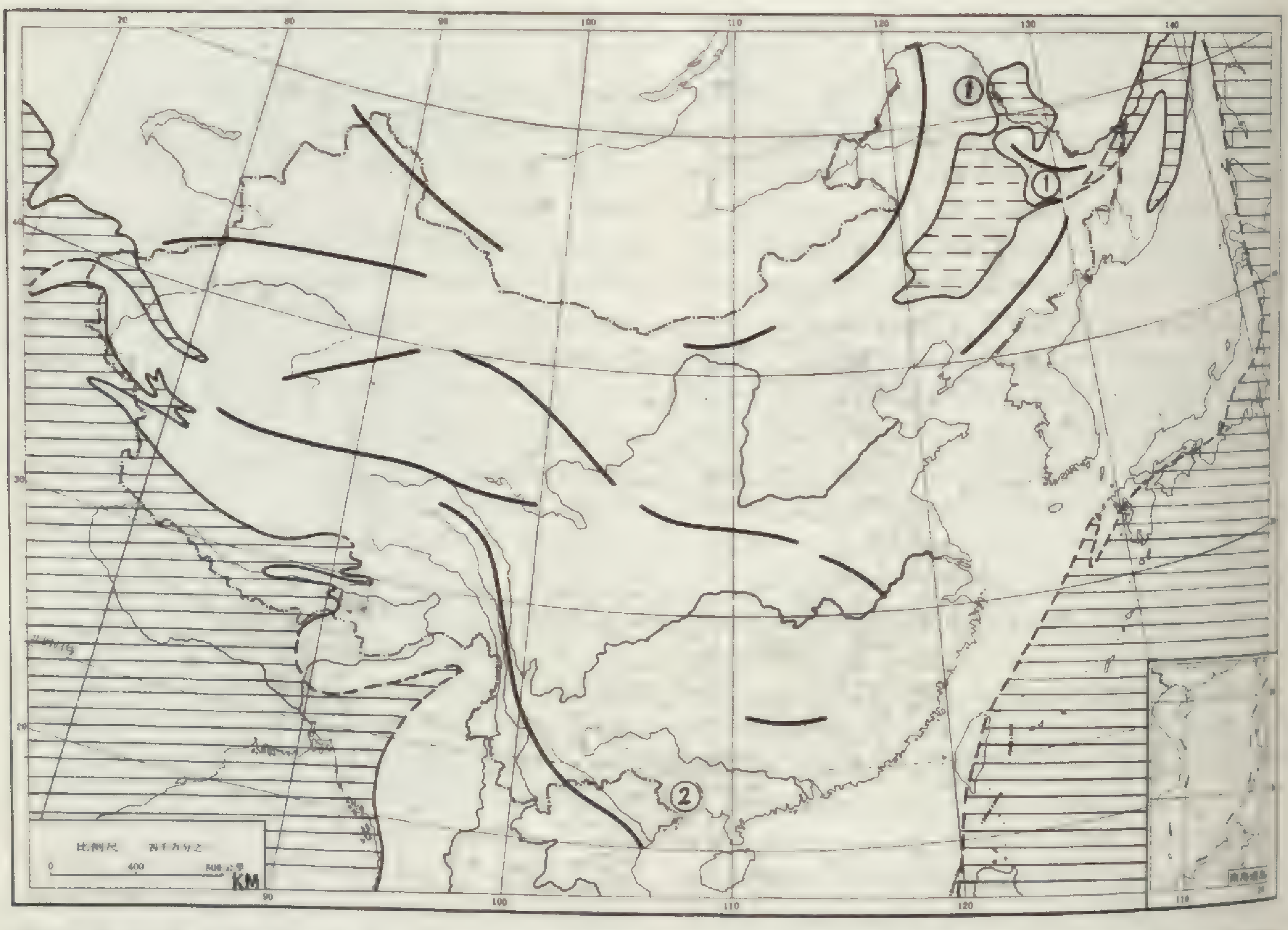

FIGURE 1. Late Cretaceous fossil localities of China: 1. Northern China; 2. Southern China. Heavy curves represent mountain ranges.

cepted as accurate, at least for portions of the time intervals. This suggests that from the middle Paleocene to present, the Pacific plate has moved 9° northward. So it is reasonable to estimate that from the late Cretaceous to the present, if the map given by Dietz and Holden (1970) is correct, Asia was relatively stable and would have moved about 10 to 13° northward.

By the late Cretaceous the northern side of China was bordered by Siberia and Outer Mongolia (Fig. 1). Ancient land of Xizang and Talimu lay on the northern coast of the Tethys. On the Pacific coast, the Sea of Japan, the Yellow Sea, the East China Sea, and the South China Sea were not yet covered by water. In western China, a series of mountain ranges, the Altai, the Tianshan, the Kunlun, the Altyn Tag, and the Qilianshan, running from west to east, already existed (Fig. 1). The watershed of the Salween-Mekong-Yangtze Rivers (the Hengduan Shan Ranges) had already formed. In the north, the Ying Shan (Inshan), the Taixinanling (Great Khingan), and the Xianxianling (Small Khingan) Mountains began to rise. In the south lay the Qinling (Tsinling), the Dabie Shan, and the Nanling Mts. Some more mountains had been folded in Jilin (Kirin) and Liaoning before Tertiary due to the effect of the collision of the Pacific and the Indian plates against the Eurasian plate. The Xizang, Yunnan-Quizhou, North China, and North Shănsi Table-Lands began to form. Among the mountains of northeastern provinces a large lake, Songhua Lake, appeared. Judged from the presence of gypsum and salt in the deposits and formation of red beds of southern China, a broad dry zone persisted there from the Mid-Jurassic up to the Oligocene, ranging from Central Asia, Yunnan to East China, south of the Qinling Ranges.

During the early Tertiary, due to the movement of the Indian plate against the Eurasian plate, all the mountain ranges in western China gradually arose. At the same time, the Xizang and the Yunnan-Quizhou plateaus were formed. Then, the Shaanxi-Shanxi and the Jiangnan plateaus came into existence due to the collision of the Pacific plate against the Eurasian plate. By the same process many mountains were folded in Zhejiang (Chekiang), Fujian (Fukien), and Guangdon (Kwangtung) of East and South China.

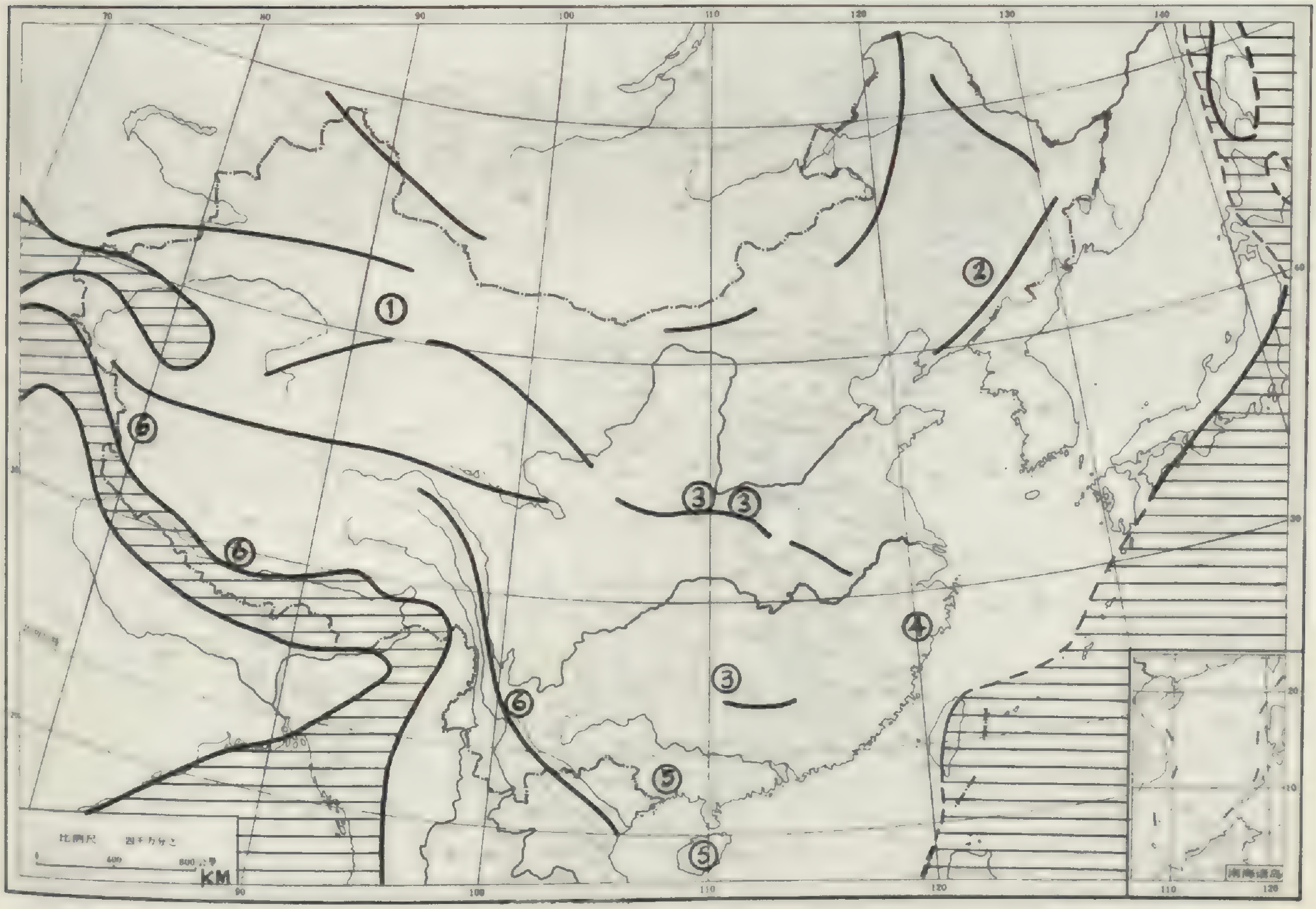

FIGURE 2. Paleogene vegetation of China: 1. Dry climate flora of northwestern China; 2. Warm temperate to subtropical deciduous and coniferous forests of northeastern and North China; 3. Dry climate subtropical floras of Central China; 4. Subtropical deciduous and evergreen forests with coniferous forests of East China; 5. Subtropical deciduous and evergreen forests associated with coniferous forests and tropical mangrove vegetation of South China; 6. Subtropical vegetation of Yunnan and Xizang.

Rising of the ocean water level led to an eastern sea coast closer to that of the present. But the coast range geosyncline extended along the Pacific margin of South and East China from Guangdong to Fujian, so the South China Bay was formed and Taiwan became submerged. In the meantime a series of large lakes appeared in the regions south of Beijing, north of Shanghai, and south of Dabie Mts. (Fig. 2).

During the late Tertiary, the topography of China became closer to that of the present. The Sea of Japan, the Yellow Sea, the East Sea, and the South China Sea began to appear. Taiwan and Hainan were uplifted to become islands. Up to the late Pliocene, many mountains of West China arose. The Himalayas and the Tanggula Ranges upheaved over 3,000 m in elevation, and the Qinghai-Xizang Plateau became higher than 2,000 m above the sea-level. The Talimu (Tarim) Basin, south of the Tianshan Ranges of Sinjiang province and the Quidam (Tsaidam) Basin of Qinghai province (Kokonor) turned into dry regions. Later on these dry regions extended further eastward up to the west part of Gansu (Kansu). Finally, the Talimu Basin became desert and some parts of Qinghai and Gansu gradually changed to semidesert (Fig. 3).

By the Quaternary, the topography of China was almost identical to that of the present but with slight differences. The Gulf of Pohai appeared in North China during the interglacial periods (Fig. 4). Hainan Island was once connected with the continent, but later a strait formed between them due to local subsidence of land. In northeastern China, the Taixinanling and the Xiaoxinanling Mountains were elevated, and in North China Taihangshan and the Inner Mongolian and the Loess Plateaus were raised. By that time the Himalayas and the Xizang Plateau were rapidly uplifted. The Xizang Plateau was only about 3,000 m in elevation in the early Pleistocene, but it reached 4,000 m in the late Pleistocene and in the Holocene went up to 4,500 to 5,500 m (Xu, 1981). At the same time, the

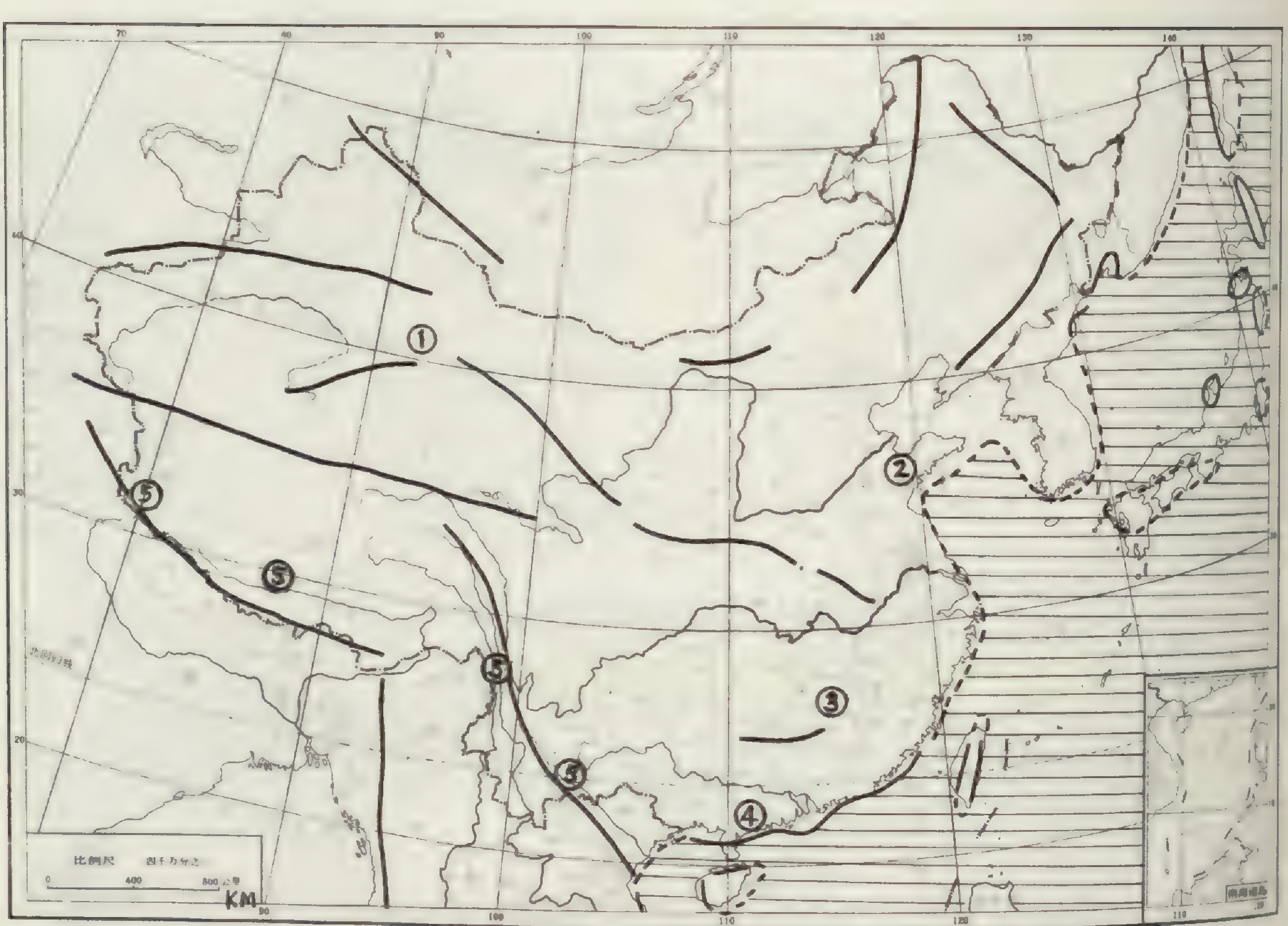

FIGURE 3. Neogene vegetation of China: 1. Temperate forests and grasslands to semidesert-desert floras of northwestern China; 2. Temperate to subtropical deciduous forests and grasslands of northeastern and North China; 3. Subtropical deciduous and evergreen forests of Central and East China; 4. Subtropical evergreen forests and tropical mangrove vegetation of South China; 5. Subtropical deciduous and evergreen forests of Yunnan and Xizang.

mountains of North China were further uplifted. Inner Mongolia, Shanxi, Shănxi, and a part of Gansu became table-lands. Loess blanketed much of this part of the country. Judging from the palynological data, I suggest that the Qinling may have reached its present altitude after the early Pleistocene. The desert of northwestern China further extended eastward. As a result of this development, western portions of Inner Mongolia and Heilongjiang became desert or semidesert.

It is well known that the Quaternary had several ice-ages. The poles of the earth were entirely covered by ice caps and glaciers occurred wherever the altitude was high enough. During the Pleistocene the ice caps increased very much in size and area, and the glaciers not only became more numerous, but also extended to cover all of Canada, the northeastern (not the southeastern) part of the United States, and most parts of western and central Europe. According to the estimate of Antevs (1928), by the time the ice sheets reached their maximum extent and thickness, the sea level would have been lowered to 100 m below the present level. Various estimates made from the present depths of shore deposits, coral reefs, etc. give a minimum figure of about 60 m (Brooks, 1950). In this way many shallow seas around the world would have disappeared. So it is reasonable to assume that all the shallow seas along the Pacific coast of China were land at least several times during Pleistocene. In addition, some of the southern Japanese islands were connected with each other and with the main continent of Asia. Taiwan and Hainan were connected with the mainland of China. Southeastern Asia and the Malaysian Peninsula were connected with Borneo, the Philippine Islands, Celebes, Sumatra, and Java. Moreover, there were also some land bridges between the Indonesian islands, the Moluccas, New Guinea, and Australia.

At present, the western Aleutians are bordered on both the north and the south by deep ocean.

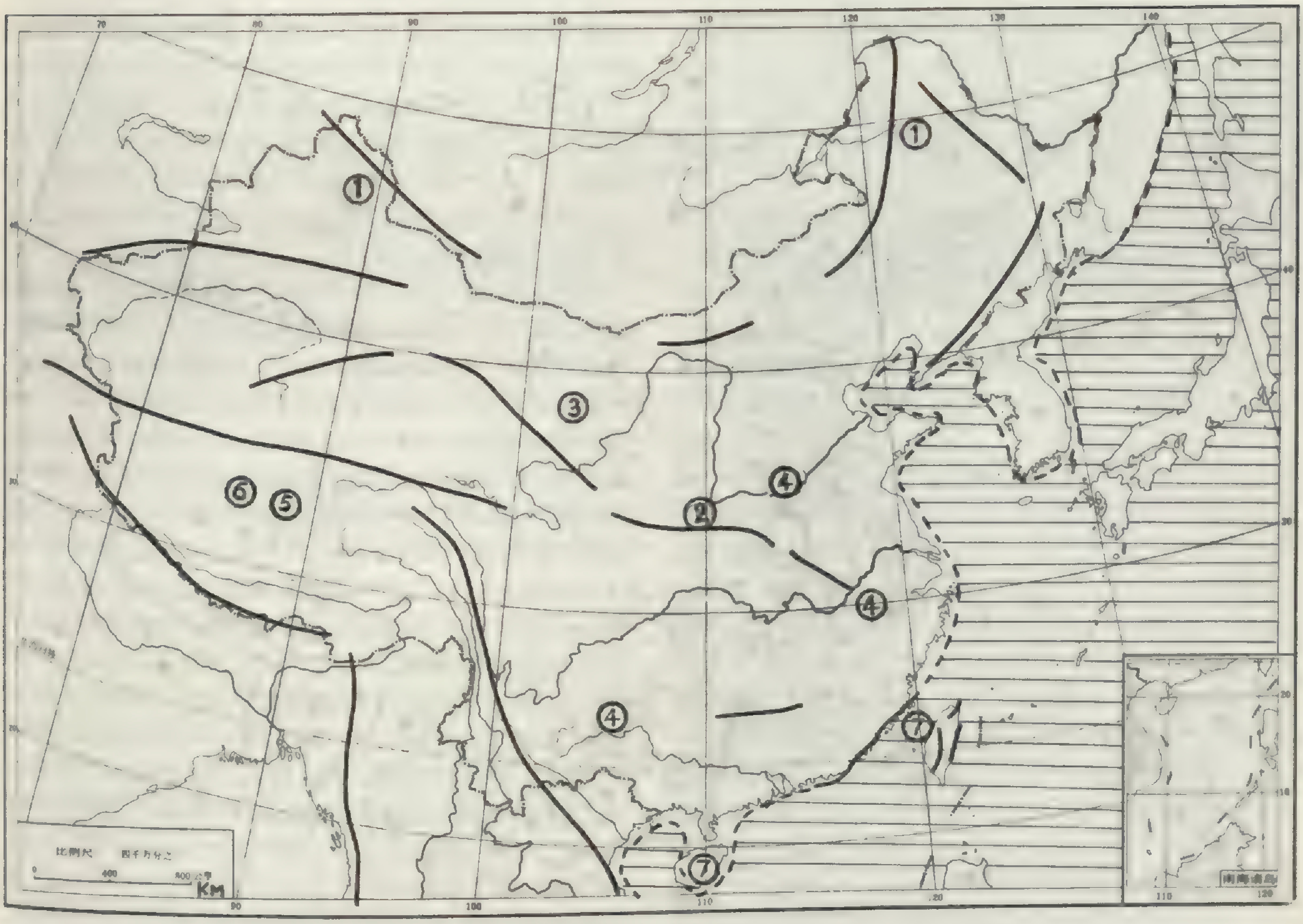

FIGURE 4. Changes in Quaternary vegetation of China: 1. Appearance of taiga; 2. Migration southward of temperate deciduous forests; 3. Expansion of dry climate flora in northwestern China; 4. Changes in vegetation due to oscillation of temperature; 5. Vegetational changes in Xizang; 6. Certain evolutionary changes accelerated; 7. Migration of plants via temporary land connections.

but the Bering Sea and the north side of the Aleutians and the Alaska Peninsula are bordered only by a shallow sea 27 to 95 m deep. So this portion of the Bering region would have become a very wide land mass favorable for plant migration between eastern Siberia and Alaska. However, during the interglacial periods, as the glacial sheets retreated and a large mass of the glaciers melted, sea level would have returned to the level of the interglacial periods, more or less like that of the present. Plant migration would have been temporarily blocked by sea between them.

CLIMATE

It is generally accepted that Cretaceous temperature was higher than that of the present. According to the estimate of Schwarbach (1963), the average annual temperature of the Late Jurassic in the world ranged between 25°C and 28°C. In the Early Cretaceous, the maximum temperature was 24°C, but in the Cenomanian (about 96 to 103 million years ago), sea temperature was reduced to 16°C. In the Coniacian-Santonian (about 80 to 90 million years ago), sea temperature rose to 22°C, but by the end of the late Cretaceous it declined again to 20°C. Saito and van Donk (1974) determined the isotopic temperature of bottom-water at the same sites around 14 to 15°C for Campanian (about 70 to 78 million years ago) and early Maastrichtian (about 68 to 70 million years ago), about 12°C higher than that of the present. It suggests a mild temperate climate in polar regions with surface-water around 14 to 15°C. Sea surface temperature declined over 2°C from the Middle to the Late Maastrichtian (about 66 to 68 million years ago), and further declined by 1.5°C from the late Maastrichtian to the early Paleocene (about 64 million years ago).

Gordon (1973) suggested that "Cretaceous oceanic circulation was an equatorial current system flowing through the Tethys and across the northwestern Pacific Ocean in a circumglobal band of warm water with its own characteristic fauna." Western winds probably existed at high

latitudes in the Northern Hemisphere, and current gyres existed as in the present. Drewry, Ramsay, and Smith (1974) claimed that the trade-wind system existed during the Mesozoic and Tertiary.

During the Late Cretaceous, China mainly lay in the tropical to subtropical region of about 5 to 40°N, but the northernmost part probably was in the warm temperate zone. Due to plate tectonic movement of the Pacific plate and the Indian plate against the Eurasian plate, China would have drifted some 10 to 13° northward, as mentioned above, from the Late Cretaceous to the Quaternary. Accompanying the rapid shifting of geographical position and uplift and the appearance of a series of great mountain ranges in the western part of China, the climate changed gradually from warm to cooler; so the basic development of the climate in China may be divided into three stages: Late Cretaceous to Eocene, Oligocene to Pliocene, and Quaternary. The annual average temperature from the Late Cretaceous to the present has decreased about 12°C.

During the Late Cretaceous, the warm Pacific current bathed the eastern shore of Asia, steadily drifting poleward with the warm Indian Ocean drifting in a northwesterly direction around the northern shore of the Tethys. Accompanied by warm winds these currents produced the warm climate in China and caused abundant rainfall in the northeastern part and less in the southern and western parts. There still was a great expansion of dry belt from southwestern, Central, South to East China. Summarizing, in China the climate of the Late Cretaceous was basically subtropical.

By Eocene time, the warm Pacific and Indian ocean currents were still present. Frakes and Kemp (1972) determined from oxygen isotopes that the mean annual temperature of the warm Pacific Ocean current along the eastern coast was 33°C and that of the warm Indian Ocean current 37°C. The mean annual temperature around Beijing was calculated to be slightly more than 20°C. At the same time, the climatic conditions in other areas were similar to those of the Late Cretaceous. Some large lakes appeared south of Beijing and southern Liaoning, so the climate of these parts was probably wetter than earlier.

In the Oligocene, the mean annual temperature of the Pacific Ocean current along the coast of southern China declined to 18°C, although the direction of the current was the same as before. The temperature of the Indian Ocean current then dropped to 34°C. The mean annual temperature of Beijing has been calculated to be about 15 to 20°C. The mean annual temperature is now about 15°C. By this time the climate of China south of the Qinling Mts. turned warm and wet and that north of the Qinling Mts. became slightly drier and less warm.

During the late Tertiary, the average annual temperature gradually dropped 7 to 10°C. Many mountains of southwestern China, such as the Himalayas—which were at least about 2,500 to 3,000 m in elevation, the Kunlun, the Altyn Tag, and the Hengduan Shan, became barriers, blocking the monsoonal winds from the Indian Ocean passing into Tibet. The climate of this part of China, such as the Talimu Basin, the Quidam Basin, Inner Mongolia, and the western part of Gansu, became drier and warmer. As a result of rapid uplift of the Himalayas, the climate of Xizang and Qinghai became drier and colder. By contrast, the eastern part of China was subjected to the moderating influences of the Indian and the Pacific Oceans and became warm and wet. Due to the barrier of the Qilian Shan and the Qinling Mts. across the middle part of China, running from west to east, cold air masses from Siberia were blocked and the climate of southern China became warm and wet. According to the results of recent investigations on the geology of China during the Pleistocene, there is no reliable evidence of glaciation on the mountains in the eastern part of China, except the Taibei Shan of the Qinling Ranges. But the temperature of northeastern China became cooler and slightly drier than before and was temperate in nature. There was a marked drop of temperature to the Quaternary. In comparing it with that of the Late Cretaceous, the average annual temperature would have declined 14 to 24°C. Judging from the plant fossils found at Weinan (109.5°E, 33.3°N) in Shănsi Province and Panxian (104.7°E, 25.8°N) in Guizhou Province, the difference in temperature between the Wisconsin Glacial Period and the present in the eastern part of China is around 8°C lower.

As the Quaternary is the most active period of the upheaval of the Himalayas and the Xizang Plateau, the climate of Xizang Plateau during the interglacial periods of early and middle Pleistocene was relatively moderate. But up to the late Pleistocene and Holocene the climate became dry and very cold. Other parts of western China also became dry and cold. However, the temperature and amount of precipitation of the

southernmost part of southwestern China and the coastal region of South China, Guangdong, and Guangxi, the Hainan Island, the southern part of Taiwan and the islands of South China Sea were tropical.

Late Cretaceous Vegetation in China

During the Late Cretaceous and Cenozoic, the Chinese floras were differentiated into two major floristic zones, the northern and the southern. The demarcation was clearly controlled by a chain of mountain ranges, running from west to east, that is, the Kunlun, the Altyn Tag, the Qilian Shan, the Qinling, and the Dabie Shan. The vegetation as a whole was subtropical.

According to Berry (1937) and Axelrod (1952), by the middle Cretaceous the floras of the world were already differentiated into Arcto-Cretaceous, Tropical Cretaceous, and Antarcto-Cretaceous provinces. The Late Cretaceous was further differentiated into two distinct floras—Boreal and Tethyan (Takhtajan, 1969)—corresponding to the Arcto- and Tropical Cretaceous Floras. The Boreal-Cretaceous flora was temperate in nature, consisting chiefly of mesophyllous deciduous trees and shrubs together with ginkgoes, conifers, and ferns. This flora was widely distributed in the northern part of North America, the Arctic, Greenland, North, Central and northeastern Europe, Kazakhstan, Siberia, the Far East of the U.S.S.R., Korea, and Japan. The Tethyan-Cretaceous flora was subtropical in nature, consisting mainly of evergreen trees and shrubs, with some deciduous, comparatively narrow-leaved forms. In this flora, Lauraceae, Aquifoliaceae, evergreen Fagaceae, and palms were characteristic, as well as Myrtaceae and Sapotaceae. It was widely distributed in the southern part of North America, southern England, southern Europe, the Baltic, the Caucasus, the southern part of the Caspian Sea, Turkman, Central Asia and the main part of China, and Outer Mongolia. In the southern part of this region, a broad, seasonally dry zone extended from Spain and north Africa, through West and Central Asia to eastern China and northern Indo-China, judged from lithological data. South of the subtropical Tethyan-Cretaceous flora lay the Paleotropical Cretaceous flora. Fossils known from Nigeria, Egypt, Syria, Iraq, and Iran indicate the existence of a tropical flora of the Malaysian type. Remains of mangrove vegetation flourished on the northern shores and islands of the Tethys (Takhtajan, 1969).

Late Cretaceous Flora of Northern China

Late Cretaceous fossils of northeastern China have been recorded from the Hunchun Group in the Hunchun Basin of Jilin and the Sungari Series of Wuyun of Heilongjiang (Fig. 1:1).

Both megafossils and microfossils were mainly of ligneous plants, though sporopollen assemblages included ferns, gymnosperms, and herbaceous plants.

Flora of the lower part of the Hunchun Group and Hunchun Basin (130°E, 42.8°N) of Jilin, of Turonian to Senonian age (95 to 67 million years ago) represents a mesophyllous deciduous forest characteristic of a warm-temperate, humid climate. In this flora the conifers *Glyptostrobus europaeus* (Brongn.) Heer and *Metasequoia cuneata* (Newb.) Chaney are very abundant. Angiosperms include *Populites* cf. *litigiosus* (Heer) Lesq., *Juglandites poliophyllus* G. et L., *Trochodendroides vasilenkoi* Iljin et Rom., *Protophyllum multinervis* Lesq., *P. haydenii* Lesq., *P.* spp., and *Leguminosites* (Guo & Li, 1929).

A similar flora of the Late Cretaceous from Wuyun (129.8°E, 49.11°N) in Heilongjiang flourished in a warm temperate to subtropical humid climate and is under investigation by Tao of our laboratory. In this flora *Osmunda greenlandica* (Heer) Brown and the conifers *Metasequoia* and *Sequoia* were predominant, associated with a few specimens of *Thuja cretacea* (Heer) Newberry. The angiosperms include *Protophyllum* cf. *microphyllum* G. et L., *Pseudoprotophyllum* cf. *dentatum* Hollick, *Betula prisca* Ett., *Alnus, Populus carneosa* (Newberry) Bell, *Ziziphus phosphoria* Krysht., *Mahonia* cf. *furnaria* Brown, *Menispermites borealis* Heer, *M. obtusiloba* Lesq., *M. kuliensis* Tanai, *Ampelopsis acerifolia* (Newberry) Brown, *Debeya tikhonovichii* (Krysh.) Krassilov, *Trochodendroides arctica* (Heer) Berry, *Tetracentron, Sorbaria, Tiliaephyllum* cf. *tsagajanicum* Kapacnorb., *Viburnum cupanioides* (Newberry) Brown, *V. antiquum* (Newberry) Hollick, *V. asperum* Newberry, *Bauhinia, Pterospermites auriculaecordatus* Hollick, *Cissus marginata* (Lesq.) Brown, *Rhus* cf. *turcomanica* (Krysht.) Kor., and *Cyclocarya.*

These fossils lived on the shore of ancient Songhua Lake. They contributed to a mesophyllous deciduous forest, with a few evergreen plants, including *Mahonia* in the forests. At present, *Bauhinia, Pterospermum, Rhus,* and *Cissus* occur in tropical-subtropical regions.

Judged from the fossils, the Late Cretaceous

flora of northeastern China belonged to the Boreal Cretaceous Flora. It contained a great many temperate taxa, such as *Alnus, Betula, Corylus, Populus, Salix, Tilia,* and *Zizyphus,* and a few warm temperate to subtropical ones, notably *Mahonia, Glyptostrobus, Metasequoia, Sequoia, Platanus, Tetracentron, Cyclocarya, Myrica, Nymphaea,* and *Trochodendroides.* The warm temperate to subtropical elements, such as *Ampelopsis, Viburnum, Sorbaria, Rhus, Cercidiphyllum,* and *Schisandra,* are quite abundant. Moreover, tropical elements, such as *Bauhinia, Cissus, Pterospermites, Dombeya, Dombeyopsis,* and *Grewiopsis,* were associated with the ancient taxa *Protophyllum, Pseudophyllum,* and *Dryophyllum.*

Altogether about 40 species have so far been recorded. Twelve of them, *Osmunda greenlandica, Glyptostrobus europaeus, Thuja cretacea, Trochodendroides arctica, T. vasilenkoi, Menispermites borealis, Betula prisca, Populites* cf. *litigiosus, Debeya tikhonovichii, Ziziphus phosphoria, Tiliaephyllum* cf. *tsagajanicum,* and *Rhus* cf. *turcomanisa* seem similar to or nearly identical with European, Central Asia, and Siberian Cretaceous plants. Eighteen of them, *Osmunda greenlandica, Thuja cretacea, Metasequoia cuneata, Trochodendroides arctica, Cercidiphyllum arcticum, Protophyllum multinervis, P. haydenii, Populites* cf. *litigiosus, Menispermites obtusiloba, Ampelopsis acerifolia, Pterospermites auriculaecordatus, Pseudoprotophyllum* cf. *dentatum, Viburnum antiquum, V. cupanioides, V. asperum, Cissus marginata, Populus carneosa,* and *Mahonia* cf. *furnaria* seem similar to the North American Cretaceous plants.

LATE CRETACEOUS FLORA OF SOUTHERN CHINA

Turning to southern China, fossils of *Brachyphyllum rhombiomaniforum* Kuo, *Cinnamomum hesperium* Knowlton, *C. newberryi* Berry, *Nectandra prolifica* Berry and *N. guangxiensis* Kuo have been recorded from the Boli Formation of Cenomanian age in the Yongning of Guanxi (Guo, 1979) (Fig. 1:2).

Palynological data show that the flora of the late Early Cretaceous to Cenomanian in Jiangsu and Zheijiang was dominated by *Classopollis* (pollen of *Brachyphyllum* and *Pagiophyllum*), *Ephedra, Quercus,* Schizaeaceae, and Ulmaceae. During this period pinaceous pollen was less common (Wang et al., 1979; Song et al., 1981). These plants indicate that a dry-climate flora flourished in this subtropical region. Of the species noted above, similar fossils have been recorded in North America, such as *Cinnamomum hesperium, C. newberryi,* and *Nectandra prolifica.*

Clearly, the Late Cretaceous flora of southern China was part of the Tethyan-Cretaceous flora.

PALEOGENE VEGETATION IN CHINA

The Chinese Tertiary flora can also be basically divided into two zones, demarcated by the same mountain ranges as those of the Late Cretaceous. The northern Paleogene floras were further differentiated into two floras and those in the south into three. These were controlled by geographical and climatic factors. At that time, China was still in a lower latitude, under a subtropical climate.

The northern Paleogene flora was composed mainly of deciduous plants, such as *Carpinus, Alnus,* associated with some evergreen species, such as *Quercus, Dryophyllum,* and conifers *Sequoia, Metasequoia, Glyptostrobus, Taxodium,* and *Torreya.*

The southern Paleogene flora, which was characterized by typical subtropical taxa, consisted mainly of evergreen trees and shrubs. The herbaceous ground cover was chiefly of drought resistant plants, such as *Ephedra* and *Schizaea.* In most cases the leading role in the forests was played by numerous Lauraceae, such as *Cinnamomum, Laurus,* and evergreen Fagaceae, such as *Quercus* (including *Cyclobalanopsis*), *Castanopsis, Lithocarpus,* and palms.

DRY CLIMATE FLORA OF NORTHWESTERN CHINA

This flora developed in Xinjiang, Qinghai, and western Gansu at the beginning of Paleogene, but later extended to western Inner Mongolia. A grassland vegetation occupied the plain at the beginning but gradually became semidesert (Fig. 2:1).

According to palynological records, by the Oligocene some *Abies* and *Picea* forests with *Tsuga* were flourishing in the high hills on the northern side of the Zhungaer Basin, as were *Cedrus* forests in the lower latitudes. Deciduous forests were composed of *Betula, Tilia, Acer, Quercus, Carpinus, Castanea, Juglans, Alnus, Pterocarya, Rhus, Carya, Ginkgo,* and *Magnolia.* Some elements of Elaeagnaceae were scattered in the foothills. The undergrowth included herbs of Plum-

baginaceae, Primulaceae, Labiatae, Compositae, and others. The drought-resistant plants, *Ephedra* and chenopods, were widely distributed on the plain (Hsu, 1956).

Some forests of *Abies, Picea, Pinus, Cedrus, Betula,* and *Quercus* lived on the hills around the Quidam Basin. Trees of Magnoliaceae and Proteaceae grew scattered in the valleys. The undergrowth included herbs of Compositae, Cruciferae, Gramineae, and others (Hsü et al., 1958).

In western Gansu, pine forests were better developed in the hills around the Jiuquan Basin. *Magnolia* and *Ginkgo* grew on hilly tracts. Drought-resistant *Ephedra* was widely distributed on the plain (Song, 1958).

WARM-TEMPERATE TO SUBTROPICAL DECIDUOUS AND CONIFER FORESTS IN NORTHEASTERN CHINA AND NORTH CHINA

This flora was the successor of the Boreal Late Cretaceous mesophytic flora of northeastern China, the eastern part of Inner Mongolia, and North China. Although no Paleocene megafossils have so far been recorded in this area, a sporopollen assemblage in Fushun (123.9°E, 41.8°N) indicates that some mesophyllous forests flourished, in which *Sphagnum, Lycopodium, Sequoia, Metasequoia,* and *Ginkgo* were present. Of the angiosperms, Ulmaceae, Juglandaceae, Betulaceae, and Myricaceae were predominant. This flora was also composed of *Pinus, Picea, Abies, Cedrus, Quercus, Ulmus, Salix, Buxus, Liquidambar, Cornus,* and *Magnolia.* The general aspect of this flora was very similar to those of the same age found in East Siberian and Sakhalin Island (Song & Liu, 1976; Sun, Du & Sun, 1980).

By the late Eocene, *Osmunda, Lygodium, Salvinia, Ginkgo, Metasequoia, Sequoia, Glyptostrobus, Torreya, Taxodium, Keteleeria, Pinus, Populus, Comptonia, Alnus, Betula, Corylus, Carpinus, Fagus, Dryophyllum, Quercus, Zelkova, Celtis, Nelumbo, Trochodendron, Cercidiphyllum, Schisandra, Cinnamomum, Lindera, Hydrangea, Hamamelites, Fothergilla, Exocarpus, Rosa, Acacia, Mimosites, Phellodendron, Ailanthus, Rhus, Acer, Koelreuteria, Meliosma, Paliurus, Rhamnus, Zizyphus, Ampelopsis, Firmiana, Fraxinus, Viburnum, Sparganium,* and *Sabalites* existed in Fushun (Fig. 2:2). Fagaceae, Betulaceae, Ulmaceae, Rosaceae, and Rhamnaceae were most abundant. Most of them are deciduous, except *Dryophyllum, Cinnamomum,* and *Sabalites.* Most genera are subtropical to warm temperate, but *Osmunda, Ginkgo, Metasequoia, Sequoia, Glyptostrobus, Torreya, Taxodium, Keteleeria, Dryophyllum, Meliosma,* and *Firmiana* are almost subtropical, and *Lygodium, Cinnamomum, Acacia,* and *Meliosma* are chiefly tropical.

In this flora, one-fourth of the species, such as *Osmunda lignitum, Alnus corylina, Betula populoides, Celtis preacuminata, Dryophyllum saffordii, Lindera antique, Hamamelites inaequalis, Rosa hilliae, Acacia aquilonia, Mimosites variabilis, Ampelopsis acerifolia, Fraxinus rupinarum, Viburnum speciosum, Sparganium antiquum, Ginkgo adiantoides, Glyptostrobus europaeus,* and *Nelumbo protolutea,* as judged from the illustrations, seem similar to the Paleocene-Eocene plants of North America. Similarly, more than one-fourth of the species appear to be similar to European, Central Asian, and Siberian plants. These include *Osmunda lignitum, Lygodium kaulfussii, Ginkgo adiantoides, Glyptostrobus europaeus, Metasequoia disticha, Taxodium tinajorum, Alnus schmahausenii, Betula subpubescens, Dryophyllum dewalquei, Zelkova ungeri, Cercidiphyllum arcticum, Lindera antiqua, Phellodendron grandifolium, Paliurus colombii, Rhamnus duensis, Fraxinus juglandina, F. rupinarum,* and *Viburnum nordenskiöldii.*

Taxodium, Sequoia, Comptonia, Fothergilla, and *Sabal* are extinct in China, but still live in North America. By this time *Metasequoia, Alangium, Trochodendron, Pterocarya, Platycarya, Zelkova, Cercidiphyllum, Cinnamomum, Koelreuteria,* and *Paliurus* existed in both northeastern China and North America. They now occur only in eastern Asia.

Middle Eocene microfossils in the coastal region of Bohai also show that the climate of North China was warm temperate, characterized by a predominance of Taxodiaceae, Betulaceae, Juglandaceae, Ulmaceae, Sapindaceae, and also *Alangium, Platycarya, Lygodium* and *Osmunda.* By late Eocene-early Oligocene, *Ephedra* and *Schizaea* were abundant there. During the middle Oligocene, *Quercus, Ulmus, Alnus, Salix,* and *Melia* became dominant, and, in the late Oligocene, Ulmaceae and Juglandaceae became predominant.

As a whole, the Paleogene flora of North China was composed of *Abies, Larix, Picea, Cedrus, Keteleeria, Pinus, Tsuga, Carya, Engelhardia,*

Platycarya, Pterocarya, Alnus, Betula, Carpinus, Fagus, Quercus, Ulmus, Celtis, Trochodendron, Nelumbo, Magnolia, Liquidambar, Melia, Elaeagnus, Tilia, Rhamnus, Nyssa, Cornus, Aralia, Symplocos, Fraxinus, and *Lonicera,* associated with some elements of Liliaceae, Chenopodiaceae, and Compositae.

DRY CLIMATE FLORA WITH SCATTERED FORESTS IN THE SUBTROPICAL ZONE OF CENTRAL CHINA

Judged from a Paleocene sporo-pollen assemblage found in Jiangxi (Sun & He, 1980), the flora was composed chiefly of Schizaeaceae, Pteridaceae, Ulmaceae, Fagaceae, Lauraceae, Moraceae, Sapindaceae, Santalaceae, Magnoliaceae, Nyssaceae, Symplocaceae, Hamamelidaceae, and the tropical families Rutaceae, Anacardiaceae, Proteaceae, Araliaceae, Sapotaceae, Meliaceae, Bignoniaceae, Olacaceae, and Palmae. The genera *Schizaea, Pteris, Ephedra, Ulmus, Hemiptelea,* and *Quercus* were most abundant, followed by *Corylus, Sorbaria, Lespedeza, Rosa,* Chenopodiaceae, Cruciferae, Leguminosae, Polygalaceae, and Lythraceae.

Up to the Eocene, *Quercus, Xylosma* (Flacourtiaceae), Anacardiaceae, Hamamelidaceae, Myrtaceae, Symplocaceae, Nyssaceae, Santalaceae, Sapotaceae, and Olacaceae were very abundant. The temperate elements *Betula* and *Juglans* were less abundant.

The sporo-pollen assemblages of Hunan and Hubei of the same ages were similar to those of Jiangxi as described above.

By the late Eocene, megafossils of *Cinnamomum* cf. *lanceolatum* Heer and *Comptonia andersonii* Florin were recorded in Hunan (Sze & Lee, 1954). Some megafossils of the form genus *Palibinia* have been found in Shǎnxi, Henan, and Hunan (Tao, 1965; Li, 1965; Liu & Kong, 1978) (Fig. 2:3). The narrowness and coriaceous texture of the leaves indicate drier sites. Associated with these in Henan are leaves of *Ulmus, Fraxinus, Sophora, Crataegus, Campylotropis, Lespedeza, Cercidiphyllum, Zelkova, Dalbergia, Zanthoxylum,* and pollen of *Ephedra, Carpinus,* Myricaceae, Taxodiaceae, Cruciferae, and Leguminosae (Liu & Kong, 1973). *Palibinia* has been found in Bembridge, Isle of Wight, England, and Turkmenia of the same age. Evidently this flora was closely connected with the subtropical Tethyan Tertiary region of southwestern Asia and south Europe.

DECIDUOUS AND EVERGREEN FORESTS WITH CONIFEROUS FORESTS IN THE SUBTROPICAL ZONE OF COASTAL REGION OF EAST CHINA

This flora covered the coastal region of Jiangsu, Zhejiang, and Fujian provinces. As mentioned above, during this period mountains arose parallel to the coast line. By Paleocene–Eocene time, some deciduous and evergreen forests chiefly of Ulmaceae (*Ulmus, Zelkova, Aphananthe, Celtus, Trema,* and *Ostrya*), Betulaceae (*Carpinus, Alnus, Corylus*), Juglandaceae (*Carya, Pterocarya, Juglans*), and Fagaceae (*Fagus, Quercus*) associated with Taxodiaceae and Pinaceae (*Pinus, Keteleeria, Cedrus, Picea, Abies*) forest flourished in these mountains. Some tropical elements of *Abelia, Rhus,* Proteaceae, Magnoliaceae, and Olacaceae were present, as judged from palynological records (Wang et al., 1979; Song et al., 1981; Petroleum Geological Exploration Team of Xijiang, 1979) (Fig. 2:4).

Up to the Oligocene, forests of Ulmaceae, Fagaceae, and Meliaceae were abundant. In this flora there were some elements of Magnoliaceae, Juglandaceae, Myrtaceae, Rubiaceae, Moraceae, Araliaceae, Betulaceae, Oleaceae, Euphorbiaceae, and Rosaceae associated with *Tilia, Rhus,* and others. By this time, herbaceous plants, such as *Convolvulvus, Gentiana, Hedyotis,* and Compositae, were present. Among the gymnosperms, Taxodiaceae became better developed than the pinaceous plants. *Ephedra* and *Schizaea* have been recorded, though not abundant. This indicates that this flora was more humid than that of Central China (Wang et al., 1979).

DECIDUOUS AND EVERGREEN FORESTS MIXED WITH CONIFEROUS FORESTS IN THE SUBTROPICAL ZONE AND MANGROVE VEGETATION ALONG THE SHORE OF THE SOUTH CHINA SEA

This area covered most parts of South China, including Guangxi and Guangong and islands of the South China Sea. By the Paleocene, the flora was composed of deciduous and evergreen forests mixed with some conifers. These forests were mainly composed of Ulmaceae, Loranthaceae, and Sapotaceae.

During the Eocene, palms became abundant. Other predominant plants were Ulmaceae (*Ulmus, Celtis*), Rutaceae, Fagaceae (*Quercus, Castanea*), Juglandaceae (*Carya, Juglans, Pterocarya*), *Liquidambar, Alnus, Salix,* and some Taxodiaceae (Sun, 1982). Megafossils of *Rhus*

(Schenk, 1883), *Osmunda, Lygodium, Palibinia, Cinnamomum, Nelumbo, Trapa, Nordenskioeldia, Goeppertia, Eucommia, Cyclocarya, Citrus, Ocotea, Dryophyllum, Nectandra,* and *Sabalites* (Guo, 1965) were recorded (Fig. 2:5).

Of the 18 species, one-third of them have been recorded from the Paleogene of North America, such as *Lygodium kaulfussii* Heer, *Osmunda lignitum* (Giebel) Stur, *Nelumbo protospeciosa* Saporta, *Nordenskioeldia borealis* Heer, and *Dryophyllum puryerensis* Berry. Others have been found in Europe, Kazakhstan, and Japan, such as *Palibinia laxifolia* Korovin, *Lygodium kaulfussii, Cinnamomum naitoanum* H. & T., *C. lartitii* Watelct, *Nelumbo protospeciosa,* and *Nordenskioeldia borealis.*

Up to the Oligocene, judged from palynological data, temperate elements, such as *Alnus, Betula, Juglans, Cedrus,* and *Ephedra,* became predominant and also included *Juglans, Quercus,* and the subtropical *Liquidambar.* The tropical *Caesalpinia* (Leguminosae) and the water fern *Ceratopteris* were well represented. Mangrove vegetation appeared along the Pacific coast. This flora was closely related to the Paleogene flora of Borneo. Many types of pollen are identical in each area, especially *Florschuetzia* (possibly pollen of *Sonneratia*).

SUBTROPICAL HIGHLAND FLORAS OF XIZANG, YUNNAN, AND GUIZHOU

Some fossils were recorded from the Xigaze Group of the Yarlung Zangbo valley (Guo, 1975) and the Qiuwu and the Menshi Series of the westernmost corner of Xizang (Geng & Tao, 1982) (Fig. 2:6), including Salicaceae (*Salix, Populus*), Moraceae (*Ficus*), Cercidiphyllaceae (*Cercidiphyllum*), Araliaceae (*Aralia*), Fagaceae (*Quercus*), Juglandaceae (*Juglandites*), Celastraceae (*Celastrus*), Leguminosae (*Cassia, Sophora*), Rhamnaceae (*Rhamnus*), Rosaceae (*Spiraea*), Marantaceae (*Phrynium*), Liliaceae (*Dianella*), Cyperaceae (*Cyperacites*), and Typhaceae (*Typha*). The age of these fossils was formerly assigned by the authors to the Late Cretaceous and Late Cretaceous to Eocene, respectively. After recent investigation by field geologists, both have been shown to belong to the Eocene (Yin, personal communication). Most of these genera now live in tropical regions. *Ficus* is pantropical. *Phrynium* is distributed in Indomalaysia and tropical Africa. *Dianella* is distributed in tropical Asia, Australia, New Zealand, and Polynesia.

Of the 23 species, half of them, as judged from illustrations, seem similar to Paleogene plants of North America, such as *Populus latior* Al. Braun, *Salix meeki* Newberry, *Juglandites sinnatus* Lesquereux, *Ficus daphnogenoides* (Heer) Berry, *F. myrtifolia* Berry, *F. stephensoni* Berry, *Cercidiphyllum ellipticum* Brown, *Rhamnites eminens* Bell, *Viburnum asperum* Newberry, *Cassia fayettensis* Berry, *C. marshalensis* Berry, and *Celastrus minor* Berry. Others, such as *Salix viminalis* L. and *Spiraea alpina* Tureq., resemble those of Europe and East Asia.

A tropical-subtropical Oligocene flora occurs in Jinggu, southern Yunnan. It is mainly composed of evergreen plants, Lauraceae (*Phoebe, Machilus* and *Nothophoebe*), and Fagaceae (*Lithocarpus, Quercus* and *Dryophyllum*). Others were of Annonaceae (*Annona*), Araliaceae (*Oreopanax*), Combretaceae (*Terminalia*), Moraceae (*Ficus*), Styracaceae (*Rehderodendron*), Leguminosae (*Cercis, Erythrophloeum*), and gymnosperms (*Cephalotaxus, Calocedrus*). Shrubs of *Rhus, Rosa, Jasminum,* and *Sorbus* were part of the understory. Similar specimens, such as *Zelkova ungeri, Myrica banksiaefolia,* and *Carya cordioides,* have been found in Europe and Central Asia, and *Oreopanax oxfordensis* and *Quercus simulata* have been recorded from North America.

Neogene Vegetation in China

By Neogene time China was at a slightly higher latitude. Neogene taxa were more modern, the flora was more complex in composition, and herbaceous plants were better developed.

TEMPERATE-WARM TEMPERATE FORESTS AND GRASSLANDS AND DESERT-SEMIDESERT FLORA OF NORTHWESTERN CHINA

This flora was developed in Xinjiang, Qinghai, and Gansu, but later extended to eastern Inner Mongolia.

By the Miocene, due to decreased temperature, *Larix* and *Picea* forests began to develop in the Altai Mts., and the alpine *Sabina* forests covered mountains of northern Xinjiang. Deciduous forest composed of *Betula, Ulmus, Salix, Populus, Juglans, Alnus, Corylus,* and *Tilia* occurred in some foothills. Grasslands with *Artemisia, Ephedra,* and chenopods covered the plains. Most parts of the Talimu Basin were covered by grassland. Some trees of Taxodiaceae, Palmae, Myrtaceae, Lauraceae, Magnoliaceae, Anacardi-

aceae, Ulmaceae, *Quercus*, and *Juglans* were scattered in the foothills north of the Talimu Basin (Hsü & Li, 1980). Subalpine coniferous forests composed mainly of *Pinus, Cedrus, Abies, Tsuga*, and *Juniperus* were flourishing on the northern slope of the Kunlun Mts. (Hsü & Li, 1980). Deciduous forests of *Quercus, Castanea*, and *Alnus* occurred in the valleys. Grasslands of chenopods, Polygonaceae, and Cyperaceae, associated with *Ephedra*, covered the plains of the Quidam Basin and Gansu (Hsü et al., 1958). After the withdrawal of the Obé Sea from Central Asia, the Mediterranean elements Tamaricaceae and Zygophyllaceae (*Nitraria* and others), migrated through Central Asia to the Quidam Basin and Gansu (Li, 1960). In certain places salt marsh vegetation appeared (Fig. 3:1).

Active orogeny of the Himalayas and other mountains in Xizang caused the climate of northwestern China to become drier than before. The alpine forests of *Larix* and *Picea*, in addition to *Abies*, were better developed in the Altai Mts. Some pine forest mixed with *Betula, Ulmus, Quercus, Corylus*, and *Tilia* appeared in the foothills. But *Picea* forests were better developed in the Tianshan, western Kunlun, and Qilian Shan, with an understory of some *Rosa* and *Spiraea* shrubs (Hsü & Li, 1980). On the plains occurred a vegetation composed of drought-resistant *Tamarix, Nitraria, Ephedra, Artemisia*, Chenopodiaceae, Polygonaceae, and Gramineae. Deciduous forests of *Populus, Salix, Ulmus, Acer, Fraxinus*, and *Celtis* were scattered in some valleys (Hsü & Li, 1980).

WARM TEMPERATE TO SUBTROPICAL DECIDUOUS FORESTS AND GRASSLANDS OF NORTHEASTERN AND NORTH CHINA

Palynological investigation shows that at the beginning of the Neogene forests of *Picea, Pinus, Carya, Fagus, Quercus, Alnus*, and *Celtis* were distributed in the Sanjiang Plain (126 to 128°E, 46 to 48°N) of northeastern China. Later, forests of *Abies, Picea, Betula*, and *Pinus* became dominant due to decreased temperature (Li, 1982).

By this time, some mesophyllous forests appeared in Shanxi and Hebei, composed mainly of Pinaceae, Betulaceae, Fagaceae, Ulmaceae, Juglandaceae, and Rosaceae. Among them some thermophilous elements such as *Carya, Liquidambar*, and *Corylopsis* were present (Li, 1982).

The late Miocene flora of Shandong (Fig. 3:2) is well represented by the Shanwang flora (Hu & Chaney, 1940; Inst. Bot. and Inst. Geol. and Paleont., 1978). It was mainly composed of deciduous trees and shrubs associated with some evergreen elements. The flora includes Fagaceae (*Castanea, Castanopsis, Quercus*), Betulaceae (*Alnus, Betula, Carpinus, Corylus*), Juglandaceae (*Carya, Platycarya, Juglans*), Ulmaceae (*Ulmus, Celtis, Zelkova*), Salicaceae (*Populus, Salix*), Moraceae (*Broussonetia*), Hamamelidaceae (*Fothergilla, Hamamelis, Liquidambar*), Rosaceae (*Crataegus, Eriobotrya, Malus, Prunus, Rosa, Spiraea*), Aceraceae (*Acer*), Anacardiaceae (*Rhus, Pistacia*), Sapindaceae (*Aesculus, Koelreuteria*), Saxifragaceae (*Hydrangea*), Leguminosae (*Albizzia, Cercis, Gleditsia, Gymnocladus, Pueraria, Sophora*), Celastraceae (*Celastrus, Euonymus*), Rhamnaceae (*Berchemia, Hovenia, Paliurus, Ziziphus*), Tiliaceae (*Tilia*), Cornaceae (*Cornus*), Ebenaceae (*Diospyros*), Bignoniaceae (*Catalpa*), Vitaceae (*Ampelopsis*), and Simarubaceae (*Ailanthus*), plus some subtropical plants of Araliaceae (*Kalopanax*), Magnoliaceae (*Magnolia*), Lauraceae (*Lindera, Litsea, Cinnamomum*), Rutaceae (*Evodia*), Euphorbiaceae (*Mallotus*), Ulmaceae (*Aphananthe*), and tropical plants of Sterculiaceae (*Commersonia*), Moraceae (*Ficus*), and Vitaceae (*Tetrastigma*).

This flora consists of 125 species, of which five, *Corylus macquarrii, Juglans acuminata, Salix angusta, Astronium truncatum*, and *Fraxinus dayana*, seem similar to those of North America. Ten species, *Amelanchier sibirica, Podogonium ochningense, Acer subpictum, Vitis romanetii, Viburnum nordenskiöldii, Corylus macquarrii, Juglans acuminata, Populus glandulifera, Salix argusta*, and *Astronium truncatum*, seem common to those of Europe, Central Asia, and Siberia. It is interesting to note that *Fothergilla* existed there, but is not now in China.

According to palynological investigation, *Ulmus* was quite dominant in this flora, and *Metasequoia, Sequoia, Glyptostrobus*, and *Pinus* also lived there (Song et al., 1964), though the conifers are not recorded as megafossils.

Up to the time of the Pliocene, judged from palynological investigations, coniferous forests of *Abies, Picea*, and *Pinus* existed in the western part of North China. Mixed forests of *Ginkgo, Cryptomeria, Pinus, Betula, Salix, Alnus, Quercus, Ulmus, Zelkova, Fraxinus*, and *Celtis* were flourishing, but many tropical trees were no longer present. Megafossils found in Taigu, Shansi,

were composed mainly of *Quercus, Ulmus, Acer, Amelanchier, Ribes,* and Leguminosae, all of which are native plants now. No taxa are known to be identical with those of North America.

SUBTROPICAL EVERGREEN AND DECIDUOUS FORESTS OF CENTRAL AND EAST CHINA

During the Miocene, the vegetation of Central and East China turned into coniferous and evergreen and deciduous forests in sharp contrast to those of the Paleogene. Forests of *Pinus, Keteleeria, Cedrus, Carya, Castanea, Quercus, Ulmus, Liquidambar,* and *Tilia* were better developed. Judged from palynological records, the coniferous forests of East China were mainly composed of *Pinus, Abies, Tsuga, Picea, Keteleeria,* and *Cedrus*. Deciduous forests were mainly composed of Ulmaceae (*Ulmus, Celtis, Zelkova*), Juglandaceae (*Carya, Juglans, Pterocarya*), Betulaceae (*Betula, Alnus, Corylus*), Fagaceae (*Quercus, Fagus, Castanea*), Hamamelidaceae (*Liquidambar, Fothergilla, Corylopsis*), and Myricaceae (*Myrica*), mixed with some evergreen trees like *Magnolia, Quercus, Symplocos,* etc. *Carya, Pterocarya, Sapindus, Ilex, Symplocos, Corylopsis, Pittosporum, Melia, Liquidambar* and some elements of Rutaceae, Euphorbiaceae, Myrtaceae, and Olacaceae existed there, representing a flora of subtropical nature. Herbaceous plants were quite abundant, mainly composed of Umbelliferae, Convolvulaceae, Cruciferae, Cyperaceae, and Gramineae (Guan et al., 1979; Song et al., 1981; Zheng et al., 1981) (Fig. 3:3).

During the Pliocene, herbaceous plants became dominant. Much pollen of Compositae (*Artemisia, Blumea, Dichrocephala, Bidens, Coreopsis, Ixeris,* and others), Amaranthaceae, Caryophyllaceae, and Chenopodiaceae have been recorded. Pollinia of Orchidaceae also appeared. Judged from palynological records, the coniferous forests were evidently reduced. Deciduous forests became dominant and were composed chiefly of *Ulmus, Celtis,* and *Quercus*. It is worth noting that the tropical *Caesalpinia, Nyssa, Buxus,* orchids, and some Annonaceae and Euphorbiaceae are occasionally recorded. Salt marsh vegetation existed in the coastal region (Zheng et al., 1981).

By this time, the flora of western Sichuan was composed mainly of *Castanopsis, Quercus,* and *Actinodaphne,* associated with some *Acer* and *Sorbus* (Guo, 1978).

SUBTROPICAL EVERGREEN FORESTS AND TROPICAL MANGROVE VEGETATION IN SOUTH CHINA

During the Miocene, forests of this region were composed mainly of *Castanopsis, Quercus, Lithocarpus, Juglans, Castanea, Carya, Pterocarya,* Moraceae, Palmae, and Hamamelidaceae. In the coastal region a vegetation rich in chenopods existed. A mangrove vegetation of *Sonneratia* appeared along the coast (Sun et al., 1981) (Fig. 3:4).

SUBTROPICAL EVERGREEN AND DECIDUOUS FORESTS ON THE YUNNAN AND XIZANG PLATEAU

By the Miocene, the vegetation of southern Yunnan was composed of Cupressaceae (*Calocedrus*), Aceraceae (*Acer*), Alangiaceae (*Alangium*), Lauraceae (*Laurus, Cinnamomum*), Leguminosae (*Albizzia, Cassia, Dalbergia, Desmodium, Sophora,* and *Pithecelobium*), Juglandaceae (*Pterocarya*), Fagaceae (*Castanea, Quercus*), Hamamelidaceae (*Distylium, Siminotonia*), and Rhamnaceae (*Rhamnella*). This flora was closely related to a flora of similar age in Vietnam (Inst. Bot. and Inst. Geol. and Palaeont., 1978).

The Miocene flora of northern Yunnan included *Pinus, Cupressus,* Fagaceae (*Dryophyllum, Quercus*), Lauraceae (*Sassafras, Phoebe, Cinnamomum*), Ulmaceae (*Zelkova*), Anacardiaceae (*Rhus, Pistacia*), and Rhamnacaee (*Paliurus*) (Fig. 3:5).

By the Pliocene an evergreen forest mixed with conifers appeared. The chief elements were the sclerophyllous *Quercus semecarpifolia, spathulata, pannosa, monimothicha,* and *gilliana*. Others were *Acer paxii, Celtis bungeana, Viburnum ovalifolium, Betula, Populus, Ulmus, Michelia,* and *Rhododendron,* associated with some Rosaceae and Leguminosae. Confers were dominant, including *Pinus yunnanensis, Cedrus deodara, Picea, Larix,* and *Tsuga*. *Pinus yunnanensis* was very abundant there, but *Cedrus deodara* had migrated to the southwestern part of the Himalayas (Tao & Kong, 1973).

During this time, the forests of northwestern Yunnan were composed mainly of Fagaceae, Lauraceae, Leguminosae, Theaceae, and Loganiaceae. About half of the plants are identical to the recent ones. Most of them belong to *Castanopsis, Ulmus, Eurya,* and *Strychnos*. In addi-

tion, many species of Rhamnaceae, Fagaceae, Anacardiaceae, Leguminosae, Rosaceae, Alangiaceae, Lauraceae, and Myricaceae also occupied the southern slope of the Himalayas. This suggests that during the Neogene there was an extensive migration of plants between Xizang and Yunnan and the northern part of the South Asian subcontinent (Tao & Du, 1982) (Fig. 3:5).

By the Miocene, vegetation of central Xizang was composed mainly of *Juglans, Sophora, Populus, Betula, Carpinus, Ulmus, Ribes, Crataegus, Quercus, Thermopsis, Rhododendron, Salix, Cedrus, Tsuga, Sabina,* and *Podocarpus*. Similar vegetation was flourishing in the western Xizang (Hsü, 1981) (Fig. 3:5).

Passing to the early Pliocene, forests of *Abies, Picea, Tsuga, Cedrus, Lithocarpus, Quercus, Fagus, Salix, Carya, Melia,* and *Ilex* were widespread in northern Xizang. It is interesting to note that pollen of some tropical elements, such as *Podocarpus* and Araliaceae and spores of the epiphytic fern *Drynaria,* were found at some sites.

Up to the late Pliocene some subalpine forests were widespread on the northern slope of the Himalayas. *Cedrus deodara* and some sclerophyllous evergreen oaks, *Quercus semecarpifolia, pannosa,* and *senescens,* were predominant. The general aspect of the flora and the floral composition were much like those of the Pliocene flora of northern Yunnan (Xu, 1981).

Quaternary Vegetation in China

The Quaternary vegetation in China did not differ very much from that of the late Pliocene. However, there were some evident changes, since the evolution of plants was rapidly progressing. The change of vegetation during this period was mainly caused by the effects of decreasing and oscillating temperature, lowering and rising of sea level, and variance in topography, especially the uplift of the Qinghai-Xizang Plateau, the Himalayas, and other mountains.

Appearance of a Cold Temperate Forest Zone in the Northernmost China

From the late Pliocene up to the late Pleistocene, some Siberian, cold-temperate taxa penetrated southward 4° to 5° to form taiga in northern Xinjiang and northern Heilungjiang. Forests of *Larix gmelini* migrated southward to-and-fro several times from the Altai Mts. This forest passed along the Beitashan Range, was widely distributed in the Dzongarian Basin, and intruded the east end of the Tianshan Range (Chang, 1959). Forests of *Larix gmelini* also migrated southward several times as far as the Sanjiang plain (Kong & Du, 1982). By the time of the Late-Glacial, *Abies-Picea* forests associated with *Betula* were developed on the plain, leaving the taiga forests flourishing in the Taixinanling and the Xianxianling Mts. (Fig. 4:1).

Shifting of the Southern Boundary of the Warm-Temperate, Deciduous-Forest Zone

The southern boundary of the warm-temperate zone shifted southward 3° to 5° during the Quaternary Period. Although the Qinling Range is an old mountain range running from west to east, across China, it was not high enough to separate climates in eastern China in the early Pleistocene. The palynological record shows that the subtropical plants *Ginkgo, Podocarpus, Cedrus, Tsuga, Pseudolarix, Cunninghamia, Pterocarya, Platycarya, Carya,* and *Magnolia* still resided in Shănxi (=Shenxi), north of the Qinling Mts. (Inst. Bot. and Inst. Geol., 1966). Only after the middle Pleistocene, were the Qinling Mts. uplifted to the present altitude, thus forming a barrier to prevent seasonal winds from the south passing over to North China. Since then, the climate of North China has become drier and cooler, and the Qinling Mts. have begun to act as a barrier between the subtropical and the warm-temperate zones of Eastern China. Accordingly, the previously mentioned subtropical plants no longer lived in North China (Fig. 4:2).

Extension of the Dry-Climate Zone of Northwestern China to North China

By the early Pleistocene the semiarid zone was limited to northwestern China. Some basins in eastern Qinhai were still covered by grasslands. Only coniferous forests of *Cedrus, Picea,* and *Pinus* and deciduous forests of *Juglans, Quercus, Populus,* and *Salix* flourished in the hills. Up to the middle Pleistocene, the dry-climate zone extended westward to North China. Then the coniferous forests were mainly composed of *Pinus* and *Picea*. *Cedrus* no longer existed in this portion of Qinhai. *Alnus* and *Populus* were the chief components in the deciduous forests. Up to the late Pleistocene, due to the effect of desiccation, the size of forests and grasslands were much reduced. Some grasslands became semidesert (Fig. 4:3).

In North China some forests of conifers and broad-leaved trees still flourished in the early Pleistocene. Grasslands were well developed into

the middle Pleistocene. During the late Pleistocene, deciduous forests and grasslands were much reduced, and their composition became simpler. The forests were composed mainly of *Ulmus, Celtis, Morus, Quercus,* and *Populus*. By this time herbaceous plants were rich in Gramineae, Chenopodiaceae, Cruciferae, and Compositae (Inst. of Botany and Inst. of Geology and Palaeontology, 1978).

CHANGE OF VEGETATION DUE TO OSCILLATION OF TEMPERATURE

During the Pleistocene there may have been as many as 17 glaciations (Heller & Liu, 1982). Due to oscillation of temperature during that time, *Abies-Picea* forests were better developed in the eastern part of China, but during interglacial periods the forests decreased in area. Fagaceae was the most common group in the subtropical and moist zone, while Ulmaceae was the dominant one in the warm-temperate and drier regions.

During the last glacial (Wisconsian) period *Abies-Picea* forests were better developed on the northern slope of the Qinling Range. *Picea wilsonii* forest once extended down to the hilly lands of 490 m in Weinan (109.5°E, 34.5°N) of Shănxi (Fig. 4:4), but is widely distributed in the hills of Hebei, Shanxi, Shănxi and northern Sichuan at an altitude of 1,600 to 2,500 m. *Abies* and *Picea* forests once flourished in the foothills around Beijing 430 to 450 m (Kong, 1976), but now these forests occur only above 1,600 to 2,000 m in this area. Fossils of *Picea* have been found in Panxian (104.7°E, 25.8°N) of western Guizhou at an altitude of 1,000 to 2,000 m, but this spruce now lives at an altitude of 2,200 to 2,400 m in northern Guizhou. By this time *Abies-Picea* forests were also widely distributed in East China. Now only a few trees of *Abies* survive as relicts in the hills of Zeijiang and northern Guangxi (Fig. 4: 4).

VEGETATIONAL CHANGES DURING THE QUATERNARY IN THE XIZANG PLATEAU

During the early Pleistocene, the Xizang Plateau was about 3,000 m in elevation. Subalpine forests of *Cedrus, Pinus, Betula, Quercus, Carpinus,* and *Alnus* were widespread in the central Himalayas, while subalpine forests of *Larix, Abies, Picea, Pinus,* and *Sabina* flourished in western and northern Xizang, and subalpine forests of *Picea* and *Sabina* occurred in northern Xizang. By that time, the xerophilous plants *Tamarix* and *Nitraria* had already migrated from the Qinghai Plateau to northern Xizang (Fig. 4: 5).

During the middle Pleistocene, the Xizang Plateau was uplifted to 3,500 m in altitude. Subalpine forests of *Picea, Cedrus, Sabina* and sclerophyllous evergreen *Quercus semecarpifolia, pannosa,* and *senescens* were widely distributed in the central Himalayas. But subalpine forests of *Pinus, Betula, Quercus, Carpinus,* and *Alnus* still occurred there. Due to decreased temperature and rainfall only few forests could survive in northern Xizang, so xerophytic plants *Ephedra, Tamarix, Nitraria, Artemisia,* and chenopods were better developed there.

As the result of uplift, as the Xizang Plateau rose to 4,000 m, few forests could survive in northern Xizang.

Passing to the Post Glacial, the altitude of the Xizang Plateau was 4,500 m in elevation, and the vegetation of most parts of Xizang became alpine steppes.

ACCELERATION OF EVOLUTION DUE TO TOPOGRAPHIC AND CLIMATIC CHANGES

The speed of evolution of the angiosperms of Xizang was accelerated by the uplift of the Xizang Plateau. Plants in Xizang adjusted to the influences of topographic and climatic changes by evolving some new genera and species. More than 32 new genera of Umbelliferae, Primulaceae, Solanaceae, Compositae, and Gramineae have recently been discovered in Xizang (Wu et al., 1981). Most of the species of Gramineae are polyploids (Liu, personal communication). At the same time, a new regional alpine flora was formed (Wu et al., 1981) (Fig. 4:6).

MIGRATION OF PLANTS BETWEEN MAINLAND OF CHINA AND THE ADJACENT ISLANDS

Lowering of sea levels caused by the withdrawal of ocean water to form the Pleistocene ice sheets caused the Pacific coast to extend eastward to the Taiwan-Ryukyu Area-Kyushu during the glacial periods. This enabled some plants from Fujian to migrate directly to Taiwan and from Guangdong to Hainan, and *vice versa* (Fig. 4:7).

THE RELATIONSHIP OF CHINESE PAST FLORAS WITH THOSE OF NORTH AMERICA

Paleobotanical records previously mentioned tell us that most of the Late Cretaceous and Paleocene-Eocene plants were widely distributed in

Laurasia. During the Late Cretaceous less than one-third appear to be similar to European, Central Asian, and Siberian species and one-half to two-thirds appear similar to North American species. By the time of Paleocene-Eocene, one-third to one-fourth of the species seem similar to those of Europe, Central Asia, and Siberia, and one-fourth to one-half seem similar to those of North America. This reflects an extensive migration between the Chinese and North American floras via Central and West Asia and Europe before the middle Eocene, as there were no effective barriers such as ocean or high mountains in these regions. By this time there was also no land bridge available in the Bering region for migration of plants between Asia and North America.

By the Oligocene most species in China were of eastern Asiatic origin. One-tenth were common with the plants of Europe and Central Asia and less than one-tenth appear to be similar to those of North America. Until the Miocene about one-tenth of the plants recorded in China were common with the European, Central Asian, and Siberian species, and only one-twenty-fifth seem similar to the North American species. Up to the Pliocene, most of the Chinese plants were of eastern Asiatic origin, only a few were common with European, Central Asian, and Siberian species, and very few appear to be similar to North American species. This means that after the Eocene Chinese vegetation was rapidly modernized by a loss of the American elements. Some Chinese Oligocene and Miocene species common with those of North America are remnants of mesophytic plants once widely distributed over all the northern hemisphere.

I agree with the view of Li (1971) that most of the present isolated and disjunct genera of eastern Asia, especially of China, and eastern North America are the remants of ancient plants widely distributed all over the northern hemisphere. I also agree with the view that the present disjunction of genera is mainly due to "Tertiary and Pleistocene extinction, except the local areas with persistence of favorable climatic conditions" as claimed by Schuster (1976).

At present, eastern North America and eastern Asia (especially the southern part of China) are two important relict temperate centers in the northern hemisphere, because in both regions there were no extensive Pleistocene glaciations, and they both have more favorable climatic conditions. However, of these two regions, eastern Asia (especially southern China) has more relict genera than eastern North America.

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VEGETATION OF CHINA WITH REFERENCE TO ITS GEOGRAPHICAL DISTRIBUTION

HOU, HSIOH-YU (HOU XUE-YU)[1]

THE PHYSICAL/GEOGRAPHICAL BACKGROUND OF CHINA'S VEGETATION

General references for this section include: Editorial Board of China's Vegetation (1980); Hou (1956, 1982).

China is situated in the eastern part of Asia, on the western coast of the Pacific Ocean. The distance from east to west measures over 5,000 km, and from north to south, over 5,500 km.

The topography of China is a three-step west-east staircase (Fig. 1). It begins with the Chinghai-Tibet Plateau, 4,000 m above sea level. Crossing Kunlun and Chilien ranges on the plateau's northern edge and the Hengtuan Mountains on its eastern edge, the land slopes away to highlands and basins mostly from 2,000 to 1,000 m above sea level; it then descends further eastward to hilly regions and plains below 1,000 m.

The summer monsoons greatly dominate the climate of the country. The southeast monsoon arising over the Pacific Ocean mainly influences the eastern half of China. The southwestern monsoon arising above the Bay of Bengal and the Indian Ocean mainly influences China's southern and southwestern regions. This is why coastal eastern China, especially the southeastern part, has comparatively heavy precipitation that is highly concentrated within a few summer months. The annual rainfall ranges from 600 to 1,000 mm in the northeast, and is mostly between 1,000 to 2,200 mm in the southeast. Atmospheric moisture decreases as one goes westward. Due to the long distance from the sea to the mountains and plateaus that obstruct the wet winds blowing in from the south and southeast, the northwestern parts of China have a low rainfall, mostly receiving an average of less than 100–500 mm annually. The land lying between the two regions mentioned above is semi-arid, having a mean annual rainfall of 300–400 mm. Thus, three vegetational regions, namely forests, steppes, and deserts, correspond to the humid, semi-arid, and arid climates (Fig. 2).

Because the northernmost point of China is at about latitude 53°N, and the southernmost one at about latitude 4°N, the tremendous difference in latitude gives China wide variation in temperature. The eastern section can be divided into four climatic zones from north to south, namely, cold-temperate, temperate, subtropics, and tropics (Fig. 3). Accordingly, there occur four vegetational regions, namely, needle-leaved deciduous forests, broad-leaved deciduous forests, broad-leaved evergreen forests, and tropical semi-evergreen seasonal and rain forests.

Because both altitude and terrain also strongly influence the climate, climatic regions are very complicated in China (Fig. 4). The greater part of the Chinghai-Tibet plateau ranging from 4,000 to 5,000 m above sea level has a cold high-mountain climate with regions of subalpine forests, alpine meadows, alpine steppes, and alpine deserts.

There is a close relationship between the character of the soil and the nature of the underlying rock. However, climate, topography, and vegetation are just as important as rock in determining the ultimate nature of the soil. Because of the variation in soil formation factors mentioned above, the soil varies greatly from place to place in China (Fig. 5). In the same climatic zone, different vegetation types can occur on different soils.

In a country like China where numerous variations occur in physical features, climatic, and soil conditions, it is not surprising that many types of vegetation are to be found.

CONCEPTS AND CLASSIFICATION OF VEGETATION

General references for this section include: Braun-Blanquet (1932); Chien et al. (1956); Küchler (1964); Tansley (1953); UNESCO (1973); Walter (1973); Warming (1909); Weaver and Clements (1938); Whitaker (1962).

Different schools of geobotanists have developed various concepts concerning plant communities (the vegetation). I maintain that a plant

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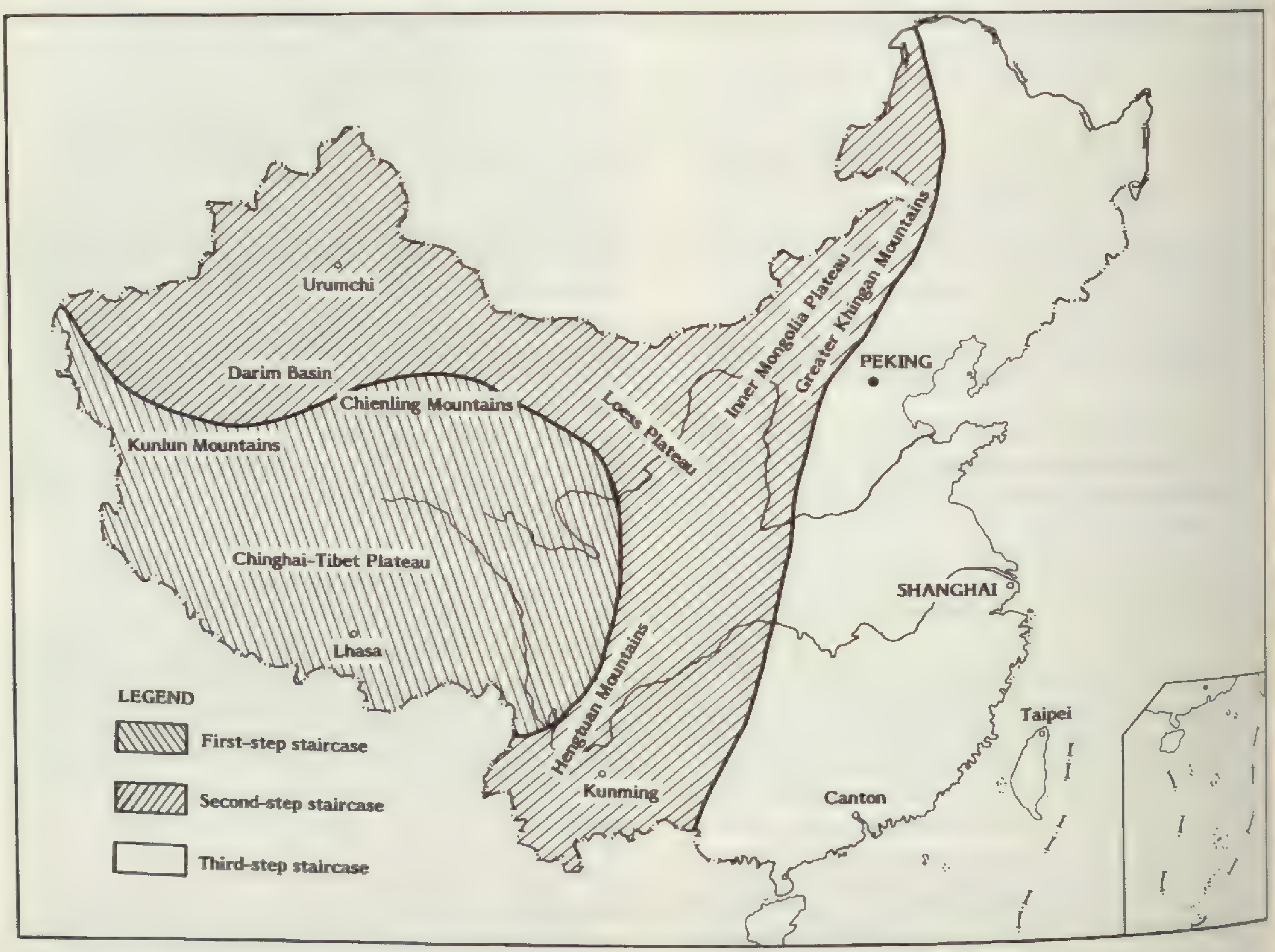

FIGURE 1. Map showing topography of China.

community, occupying a certain space, is an aggregate of plants occurring together in a common habitat. The groups of associated plants are to a certain extent similar in structure (including population, stratum, synusium), floristic composition, external appearance of the dominant species, and intimate functional interrelationships among each other, and in their relationship to environmental factors. From this viewpoint, a plant community can be considered to be a system that includes not only the plants of which it is composed, but also the natural geographic environment of habitat that forms a recognizable self-containing entity. It also means that either the climax or serial stages, and either natural or man-made ones are all considered to be part of the plant community (Hou, 1960, 1979, 1982).

Based on the plant community concept just given, the following four criteria should be thoroughly considered when classifying vegetation: (a) life or growth forms of dominant plants; (b) strata and synusia; (c) dominant floristic composition with the help of character (indicator or diagnostic) species; (d) habitat or environment.

Only two of the higher vegetational categories in China are used in this paper. The highest one can be called "vegetation type," which corresponds approximately to "formation class" suggested by UNESCO (1973). This unit refers to the plant community in which the dominant plants in the dominant layer have a common life or growth form, including needle-leaved forests, broad-leaved forests, shrubs and coppicelands, deserts and xerophytic shrubs, steppes and savannas, meadows, and swampy herbaceous vegetation.

The vegetation category mainly described in this paper can be called "formation class," which is to a great extent similar to the term "formation group" (UNESCO, 1973). This category refers to communities that have a certain common floristic composition, including families and genera, in addition to the same life or growth forms of their dominants. The geographical distribution of this category corresponds essentially to a certain latitudinal, longitudinal, or vertical zonation. Thus, supplementary terms referring to climate, soil, and landforms are added to the names to help in the identification of a given category.

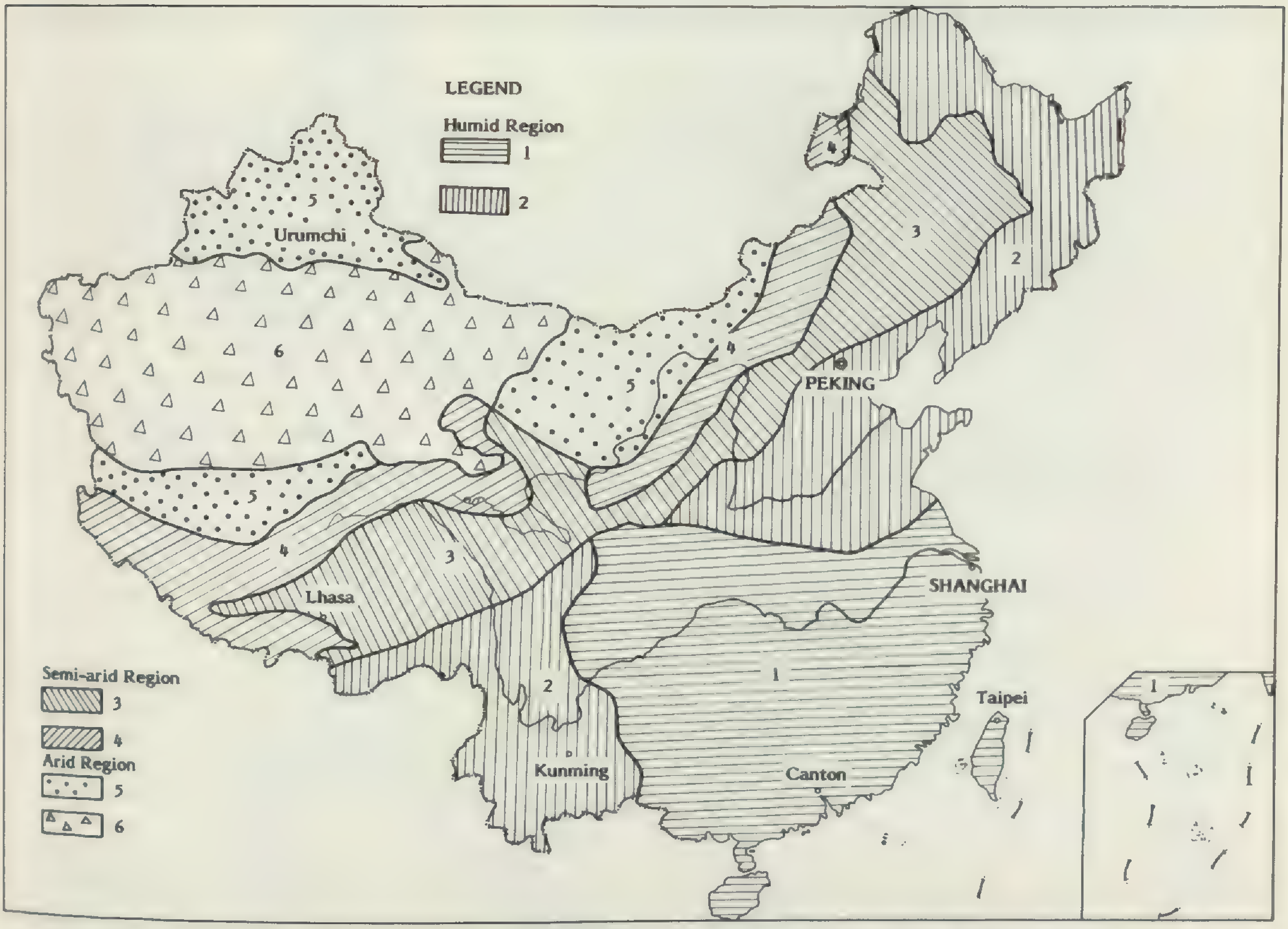

FIGURE 2. Map showing regions of atmospheric moisture of China: 1) Humid region with non-distinct dry season; 2) Humid region with distinct dry season; 3) Semi-humid region; 4) Semi-arid region; 5) Arid region; 6) Extremely arid region.

VEGETATION TYPES OF CHINA AND THEIR GEOGRAPHICAL DISTRIBUTION

NEEDLE-LEAVED FORESTS

1. *Needle-leaved deciduous forests (light taiga) of the cold-temperate zone or on the mountains of the temperate zone.* Reference: Chang (1955). Larch forests, being light-demanding, can endure a greater degree of dryness than spruce and fir forests. They can be found on either dry, sunny slopes or in moist valleys and lowlands. *Larix gmelini* forests occur chiefly on the Greater Khingan Mountains in extreme northern China, where the climate is continental boreal. These forests have an undergrowth of dwarf shrubs, the drier with *Vaccinium vitis-idaea* and the wetter with *Ledum palustre*. In the Altai, in northwesternmost China, the predominant tree is replaced by *Larix sibirica*, often growing with *Pinus sibirica*. *Rhododendron dauricum* appears frequently in the shrub layer of this forest (Fig. 6).

2. *Needle-leaved evergreen forests (dark taiga) on mountains of the temperate zone.* References: Chen et al. (1964); Chow and Li (1964); Integrated Survey Team of Sinkiang and Institute of Botany, Academia Sinica (1978); Teng (1947). The shady coniferous forests dominated by *Picea obovata*, *Abies sibirica*, and *Pinus sibirica* are confined to the northwesternmost corner of the Altai Mountains, whereas those of *Picea jezoensis*, *P. koraiensis*, *Abies nephrolepis*, *A. holophylla*, and *Pinus sylvestris* var. *mongolica* are extensively distributed in the northeastern mountains of China. The climate of the two above-mentioned regions is much more humid than that of places where only spruce forests occur. On the mountains of Tianshan, Chilienshan, and Honan, which are situated in the central part of the arid desert region, only spruce forests, dominated by *Picea shrenkiana* and *P. crassifolia*, but no fir forests, are found (Figs. 7, 8).

3. *Needle-leaved evergreen woodlands on semi-arid sandy soil of the temperate zone.* Reference: Zhao (1958). The precipitation of the semi-arid steppe, which ranges from 300 to 400 mm yearly,

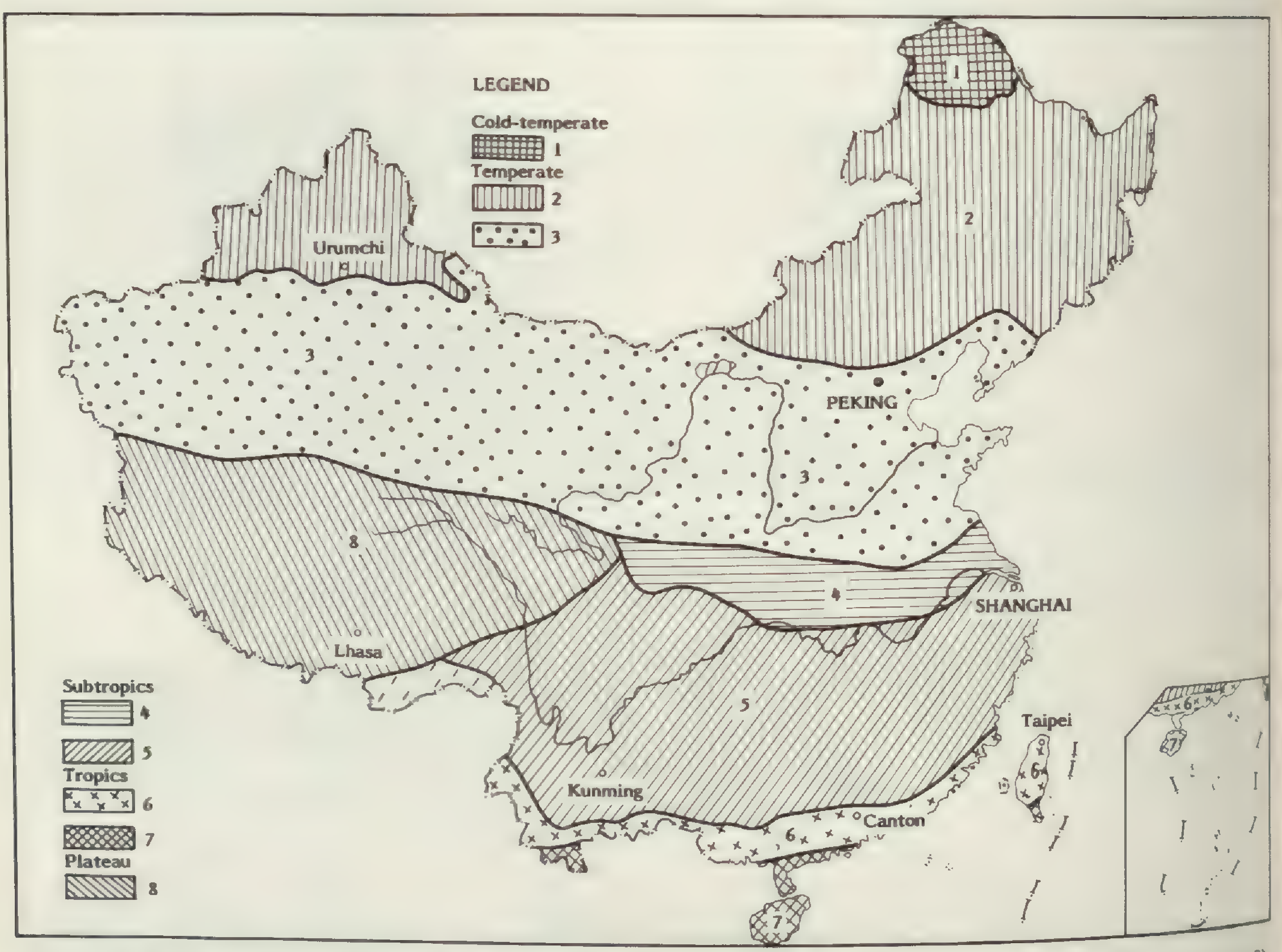

FIGURE 3. Map showing regions of atmospheric warmth of China: 1) Cold-temperate; 2) Temperate; 3) Warm-temperate; 4) Transitional subtropics; 5) Subtropics; 6) Transitional tropics; 7) Tropics; 8) Cold high-mountain climate.

is much less than in humid areas. However, the sandy soil can retain larger amounts of rainwater than the loamy soil on which grasses grow. More or less open and scattered woodlands dominated by *Pinus sylvestris* var. *mongolica* grow on the sandy soils. This type of woodland has an undergrowth of steppe species and not forest species (Fig. 9).

4. *Needle-leaved evergreen forests of the temperate zone.* These forests are distributed on the hills and mountains of the North China Plain that are under the influence of the summer monsoon. One type of forest, consisting of *Pinus tabulaeformis* inland and *P. densiflora* along the coast, occurs on acid brown soils. Another group, dominated by *Platycladus orientalis*, is seen on neutral or calcareous Korichnevie soils. This type of forest is usually associated with deciduous broad-leaved trees and shrubs (Chen et al., 1954, 1965; Chow, 1963) (Fig. 10).

5. *Needle-leaved evergreen forests of subtropical and tropical zones.* References: Chow (1957); Ho and Chen (1963); Kiang (1958); Wu (1955). These forests are composed of warm-loving needle-leaved trees belonging to Pinaceae, Taxodiaceae, and Cupressaceae, and are usually accompanied by some evergreen broad-leaved trees and shrubs. Forests growing on acid soils include *Pinus massoniana, P. yunnanensis, P. armandii*, and *Cunninghamia lanceolata* in the subtropics, and *Pinus khasya* and *P. finlaysoniana* in the tropics. The montane *Pinus taiwanensis* forests and mixed *Cathaya argyrophylla* forests are also found on acid soils in the subtropics. Another group, including *Cupressus funebris* and *C. duclouxiana*, thrives on limestone soils (Figs. 11, 12, 13).

6. *Needle-leaved evergreen forests on mountains (subalpine conifers) of subtropical and tropical zones.* References: Chiang (1963); Editorial Board of Szechuan's Vegetation (1980); Teng (1948). Because air temperature decreases with increasing altitude, on mountain ranges between 2,500 to 4,000 m above sea level in subtropical

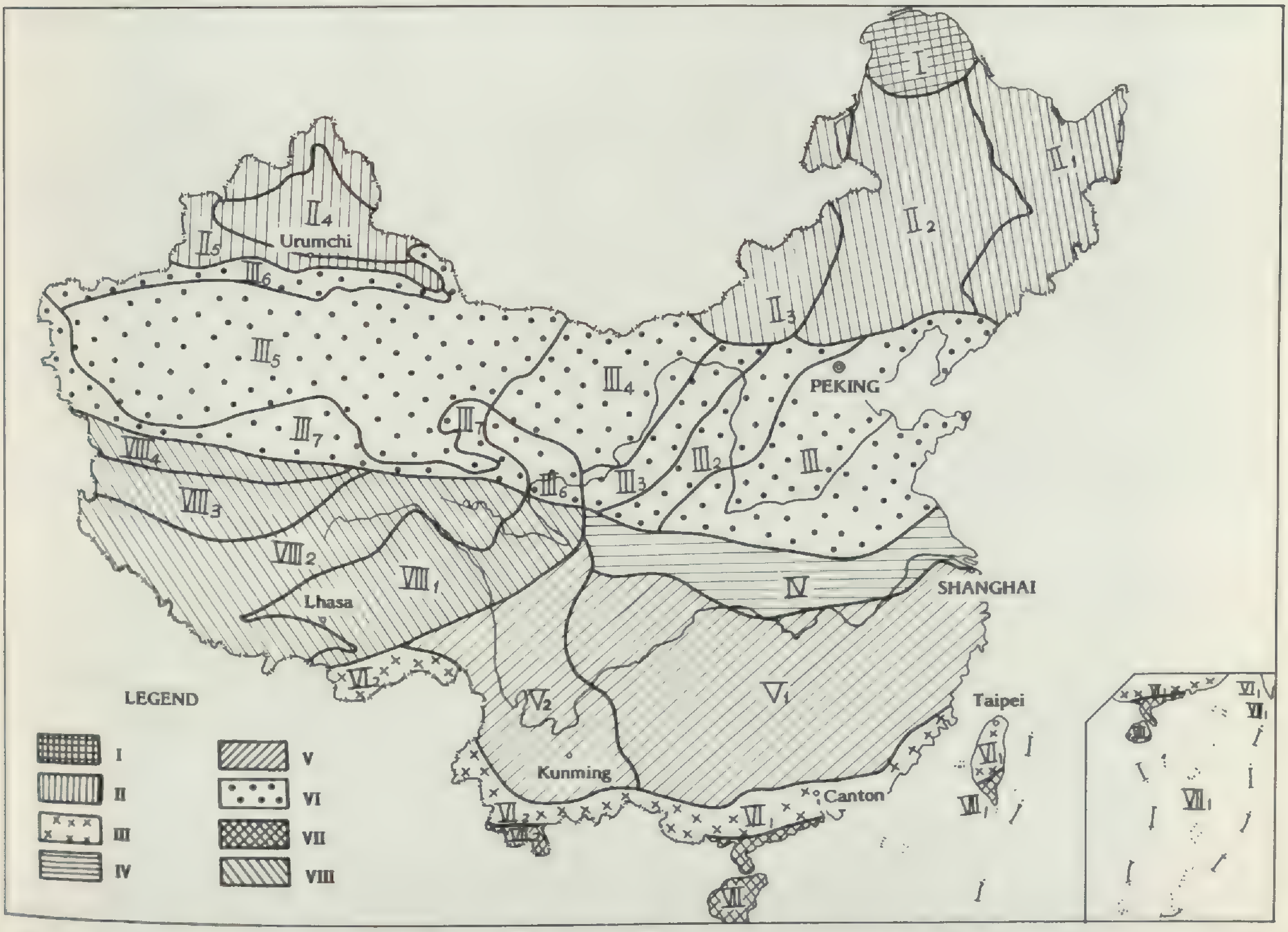

FIGURE 4. Map showing climatic regions of China: I) COLD-TEMPERATE ZONE—Humid region; II) TEMPERATE ZONE—II1. Humid region with distinct dry season, II2. Semi-humid region, II3. Semi-arid region, II4. Arid region with evenly-distributed rainfall, II5. Semi-arid and humid montane region; III) WARM-TEMPERATE ZONE—III1. Humid region with distinct dry season, III2. Semi-humid region, III3. Semi-arid region, III4. Arid region, III5. Extremely arid region, III6. Montane semi-arid region, III7. Montane extremely arid region; IV) TRANSITIONAL SUBTROPICS—Humid region with non-distinct dry season; V) SUBTROPICS—V1. Humid region with non-distinct dry season, V2. Humid region with distinct dry season; VI) TRANSITIONAL TROPICS—VI1. Humid region with non-distinct dry season, VI2. Humid region with distinct dry season; VII) TROPICS—VII1. Humid region with non-distinct dry season; VII2. Humid region with distinct dry season; VIII) COLD HIGH-MOUNTAIN REGION IN SUB-TROPICAL ZONE—VIII1. Semi-humid region, VIII2. Semi-arid region, VIII3. Arid region, VIII4. Extremely arid region.

and tropical zones, climatic conditions are found that, in some ways, resemble those of the cold-temperate zone. Because of this, evergreen coniferous forests consisting of fir, spruce, and pine can survive on the mountains at low latitudes. Although there are obvious similarities between the mountain climate of the subtropics and tropics and that of the cold-temperate zone, there are also many differences. On southern mountains the day temperatures in spring and autumn are higher and the light and heat intensity at midday are much greater throughout the year. In addition, the precipitation and humidity are much higher than those of the temperate zone. It is small wonder that the southern subalpine conifers have the following characteristics: (a) There are many species of fir and spruce, namely, *Abies faxoniana, A. georgei, A. forrestii, A. faberi, A. fargesii, A. cheniensis, A. squamata, A. delavayi, A. spectabilis, A. kawakamii, Picea asperata, P. purpurea, P. likiangensis, P. brachytyla, P. morrisonicola, P. spinulosa*; (b) The tree layer is associated with evergreen, broad-leaved *Quercus* and *Rhododendron* species, as well as *Tsuga chinensis* and *T. dumosa*, which are not found in the northern evergreen conifer forests; (c) In the shrubby layer there are no arctic plants, such as *Vaccinium vitis-idaea* and *Ledum palustre*, but rather higher evergreen shrubs such as *Rhododendron* and *Quercus* species, as well as bamboo

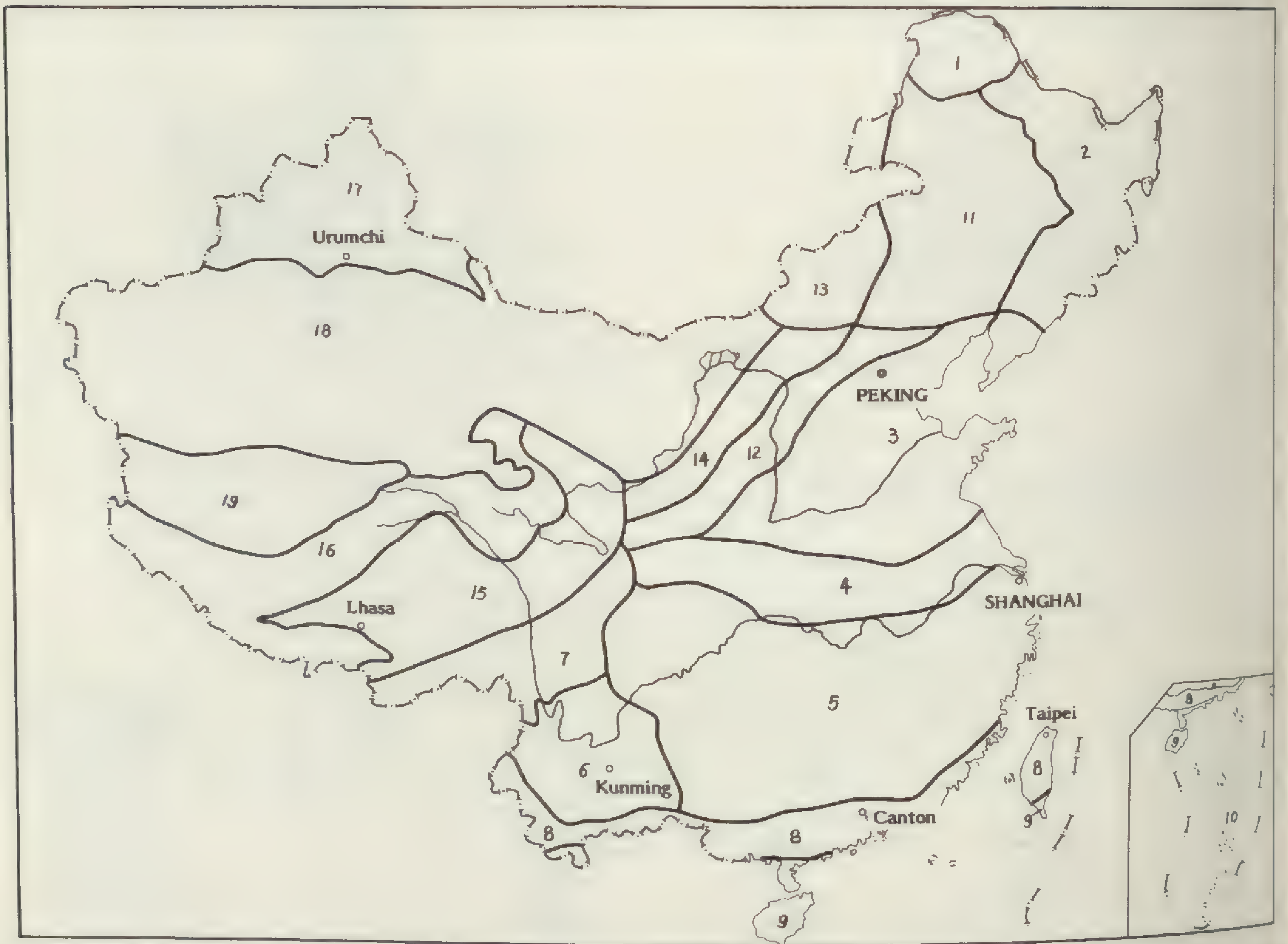

FIGURE 5. Map showing soil regions of China. FOREST SOIL REGIONS: 1) Brown conifer soil region; 2) Dark brown soil region; 3) Brown soil, Korichnevie soil, alluvial soil region; 4) Yellow-brown soil, Yellow-Korichnevie soil region; 5) Yellow and Red Earth, Purple soil, Rendzina soil region; 6) Red earth region; 7) Subalpine conifer soil region; 8) Lateritic soil region; 9) Laterite region; 10) Phosphorus lime soil region. GRASSLAND SOIL REGIONS: 11) Chernozem soil region; 12) Ziero-Korichnevie soil region; 13) Chestnut soil region; 14) Zierozem soil region; 15) Cold high-mountain meadow soil region; 16) Cold high-mountain steppe soil region. DESERT SOIL REGIONS: 17) Gray-brown desert soil region; 18) Brown desert soil region; 19) Cold high-mountain desert soil region.

shrubs such as *Sinarundinaria* and *Pleioblastus* (Fig. 14).

BROAD-LEAVED FORESTS AND WOODLANDS

1. *Mixed broad-leaved deciduous and needle-leaved evergreen forests of the temperate zone.* References: Chen et al. (1964); Chow and Li (1964); Liu (1955). The mixed forests belong to the transitional type of vegetation between evergreen conifer and deciduous broad-leaved forests. They grow on acid dark-brown soils on the northeastern mountains of China. The forests are characteristically rich in floristic composition and contain some relicts. The deciduous broad-leaved trees mainly belong to the Ulmaceae, Aceraceae, Leguminosae, Tiliacae, Juglandaceae, Oleaceae, Salicaceae, Araliaceae, etc. The following trees can be noted as representative: *Ulmus propinqua, Maackia amurensis, Fraxinus mandschurica, Tilia amurensis, T. mandschurica, Acer mono, Juglans mandschurica, Populus davidiana, P. koreana, Betula platyphylla, Quercus mongolica, Carpinus cordata, Phellodendron amurense.* The evergreen conifers are usually dominated by *Pinus koraiensis,* frequently by *Abies holophylla,* and rarely by *Taxus cuspidata* (Fig. 15).

2. *Broad-leaved deciduous forests of the temperate and subtropical zones.* References: Chen (1958); Chen et al. (1965); Numata (1974). The broad-leaved deciduous forests (known as summer-green forests) in China are mainly composed of trees belonging to the Fagaceae, Aceraceae, Tilliaceae, Oleaceae, Ulmaceae, Leguminosae, Juglandaceae, and Betulaceae. Because of the influence of a continental climate in North China, these forests differ from those in Japan and the

FIGURE 6. *Larix gmelini* forest growing on acid podzolic soil in the Greater Khingan Mountains is the typical vegetation of cold-temperate regions.

eastern United States in the absence of beeches (*Fagus* spp.). These humid-loving trees are confined to the humid subtropics in China. This type of vegetation can be classified into two groups, namely deciduous oak forests and mixed hardwood forests. The oak forests are found in relatively open and light habitats. The sequence of horizontal distribution of the dominant oaks in the temperate zone from north to south is as follows: *Quercus mongolica, Q. liaotungensis, Q. aliena, Q. dentata, Q. aliena* var. *acuteserrata, Q. variabilis, Q. acutissima, Q. glandulifera.* The second group of forests has no dominant species, but is composed of mixed hardwoods. The mixed

FIGURE 7. (Upper) At altitudes between 1,100 and 1,800 m on the Changpai Mountains, needle-leaved evergreen forest dominated by *Abies nephrolepis* and *Picea jezoensis* associated with its secondary growth. *Betula platyphylla*, is found on the lower slopes.

FIGURE 8. (Lower) At about 3,000 m altitude in northern Tienshan of the desert region, *Picea shrenkiana* forest is found on shady slopes and mountain steppe on sunny slopes.

FIGURE 9. (Upper) In the semi-arid region sandy soil can retain larger amounts of rainwater than the loamy soil on which grasses grow, so that on the sandy soil grows scattered woodland which is dominated by *Pinus sylvestris* var. *mongolica* with an undergrowth and ground cover of steppe vegetation.

FIGURE 10. (Lower) In the warm-temperate region, deciduous oak forest without beech growing on slightly acid soil is typical. However, *Pinus tabulaeformis* forest with an undergrowth of *Cotinus coggygria* var. *cinerea* also occurs here.

FIGURE 11. (Upper) After cutting of the broad-leaved evergreen forest in the subtropical region, *Cunninghamia lanceolata* forest (upper slope) and *Phyllostachys pubescens* (lower slope) take over.
FIGURE 12. (Lower) *Pinus massoniana* forest with *Rhododendron simsii* as an undergrowth is a secondary growth of the broad-leaved evergreen forest.

FIGURE 13. (Upper) *Cupressus funebris*, a calcium-loving tree, is the secondary growth of the mixed deciduous and evergreen broad-leaved forest on limestone soil.

FIGURE 14. (Lower) *Picea fabri* forest mixed with *Tsuga chinensis* is seen on the western mountains in the Szechuan Basin from 2,000 to 3,000 m elevation.

forests, growing on acid soils in shady and moist slopes or valleys, consist of *Acer* and *Tilia* species, *Fraxinus mandshurica, Ulmus propinqua, Betula platyphylla,* etc., whereas those growing on calcareous or limestone soils are composed of *Ulmus pumila, U. parvifolia, Celtis sinensis, C. bungeana, C. julianae, Zelkova schneideriana, Pteroceltis tatarinowii, Pistacia chinensis, Sophora japonica, Broussonetia papyrifera, Tilia mongolica, Dalbergia hupeana,* and *Ailanthus altissima* (Fig. 16).

3. *Montane microphyllous deciduous forests of temperate and subtropical zones.* Dominant trees of these forests include species of *Betula* and *Populus*. They are usually secondary, replacing cold-temperate or subalpine conifers after felling or fires. *Betula platyphylla* forests are distributed in the cold temperate zone and on mountains of the temperate zone, whereas the forests dominated by *Betula albo-sinensis* and *B. platyphylla* var. *szechuanica* frequently occur on the mountains in the subtropics. However, *Betula ermanii* often forms pure, virgin stands located at the upper limit of montane evergreen conifer forests in the temperate zone, and its lower limit can reach 1,000 to 1,800 m in the northeastern mountains of China. *Populus davidiana* can accompany *Betula platyphylla*; however, it can also be found in areas where the climate is warmer (Fig. 17).

4. *Microphyllous deciduous woodlands of the temperate zone.* References: Chen and Chow (1957); Ching (1959). There are two groups of this type of woodland. One type is distributed along the rivers of the arid region and is dominated by *Populus euphratica* (*P. diversifolia*). This species is widespread on the flood plain of the Darim River, which is fed by water from the glaciers and snows of the high surrounding mountains. It also is frequently encountered in a limited area on river banks in all desert regions. The soil in which *P. euphratica* grows is slightly saline with a water table of about 1 to 3 m. Another species is *Populus pruinosa*, found on soils with a lower salt content. *Elaeagnus angustifolia* woodland also is found on saline soil. *Ulmus pumila* woodland, which occurs more frequently on sandy soil in the semiarid steppe region, sometimes also is found in desert regions that have a water supply (Fig. 18).

5. *Mixed broad-leaved deciduous and evergreen forests on limestone soils of the subtropical zone.* References: Chow (1957); Chu and Wen (1953); Wang (1956). Because limestone has excessive drainage through sinkholes, and because rock surface temperature fluctuates greatly between day and night in the subtropics, the local soil climate is comparatively dry. For this reason, the mixed forests consist of a mixture of calcium-loving, xerophilous, deciduous trees. Most belong to the Ulmaceae, Cornaceae, Juglandaceae, Moraceae, Leguminosae, Sapindaceae, Anacardiaceae, Rhamnaceae, etc. The most common evergreen broad-leaved trees are *Cyclobalanopsis* (Fagaceae), *Cinnamomum* (Lauraceae), *Osmanthus* (Oleaceae), *Eriobotrya*, and *Photinia* (Rosaceae) (Fig. 19).

6. *Mixed broad-leaved deciduous and evergreen montane forests on acid yellow-brown soils of the subtropical zone.* References: Editorial Board of Szechuan's Vegetation, 1980; Jian et al., 1975; Kiang, 1958; Wang, 1964. This type of mixed montane forest is widely distributed on mountain slopes at 1,000 to 1,900 m level in the humid subtropics. Because of lower temperatures on mountains, the warm-loving evergreen species of broad-leaved evergreen forests are replaced by the cold-resistant ones, mixed with deciduous broad-leaved trees. The trees of the mixed forests belong mainly to the Fagaceae, Aceraceae, Betulaceae, Hamamelidaceae, Styraceae, Araliaceae, Magnoliaceae, Lauraceae, Theaceae, Ericaceae, Symplocaceae, Anacardiaceae, Rosaceae, Oleaceae, and Tiliaceae. These forests are charactized by the presence of the humid-loving trees, including *Fagus engleriana*, *F. longipetiolata*, and *F. lucida*, species that are not seen in the temperate zone of China. It should be noted that these forests embrace many characteristic species such as *Cercidiphyllum japonicum* var. *sinense, Tetracentron sinense, Bretschneidera sinensis, Davidia involucrata, Camptotheca acuminata, Nyssa sinensis, Aesculus chinensis, A. wilsonii, Liriodendron chinense,* and *Emmenopterys henryi* (Fig. 20).

7. *Broad-leaved evergreen forests of the subtropical zone.* References: Editorial Board of Szechuan's Vegetation (1980); Jian et al. (1975); Lin et al. (1965); Liu (1939); Shan and Liu (1963). Broad-leaved evergreen forests represent zonal vegetation found in areas with distinct dry seasons on mountains below 1,100 m in the eastern humid subtropics and on mountains between 1,500 and 3,000 m in the western subtropics or the Yunnan Highland. These forests can be classified as belonging mainly to two groups. One group contains evergreen oak forests, composed mainly of *Cyclobalanopsis, Castanopsis,* and

FIGURE 15. (Upper) Mixed broad-leaved deciduous and needle-leaved evergreen forest is found on the Changpai Mountains, between 500 and 1,100 m elevation. *Pinus koraiensis* is the typical conifer, whereas the broad-leaved trees include *Ulmus, Acer, Tilia, Fraxinus, Phellodendron, Carpinus,* and *Juglans.*

FIGURE 16. (Lower) At the foot of the Changpai Mountains at 200 to 500 m elevation *Quercus mongolica* forest is seen on sunny slopes.

FIGURE 17. (Upper) *Betula ermanii* occurs at the upper limit of forest lying between 1,800 and 2,000 m elevation in the Changpai Mountains of the temperate region.

FIGURE 18. (Lower) Gallery woodland dominated by *Populus diversifolia* is frequently distributed on meadow soil with ground water at a depth of several meters.

FIGURE 19. (Upper) In the subtropical region on limestone hills, mixed broad-leaved deciduous and evergreen forest is frequently found. The calcium-loving deciduous trees belong mostly to the Ulmaceae, Anacardiaceae, Sapindaceae, and Moraceae. The most common evergreen broad-leaved trees are *Cyclobalanopsis* (Fagaceae), *Cinnamomum* (Lauraceae), *Osmanthus* (Oleaceae), and *Eriobotrya* (Rosaceae).

FIGURE 20. (Lower) Mixed broad-leaved deciduous and evergreen forest mixed with beech is found at about 1,800 m elevation in the mountains of the western Szechuan Basin.

Lithocarpus, which occur in the northern subtropics. The dominant members of this group in the eastern region include *Cyclobalanopsis glauca, Castanopsis eyrei, C. sclerophylla,* and *Lithocarpus glaber,* and are often intermingled with *Fagus lucida* and *F. longipetiolata.* In the western subtropical region, the dominant species of evergreen oaks include *Cyclobalanopsis glaucoides, C. delavayi, Castanopsis delavayi, C. orthacantha, Lithocarpus dealbatus,* but without species of *Fagus.* The second group consists of mixed evergreen broad-leaved forests, dominated by warm-loving species of *Castanopsis,* as well as those of Lauraceae and Theaceae. In the eastern region, the dominant trees are *Castanopsis hysterix, C. carlesii, C. faberi, C. armata, C. chinensis, C. concinna, C. fissa, Schima superba, Adinandra bockiana, Polyspora axillaris* (*Gordonia axillaris*), *Ternstroemia gymnanthera, Hartia sinensis, Eurya loquaiana, E. pseudopolyneura, Cinnamomum parthenoxylum, C. japonicum, C. chingii,* and *Phoebe bournei.* In addition, there are some species of Hamamelidaceae and Elaeocarpacaeae, which are frequently mixed with species of *Fagus.* In the western subtropical region, the forests consist mainly of *Castanopsis orthacantha, C. hystrix, Machilus yunnanensis* var. *duclouxii, M. kurzii, Actinodaphne reticulata, Schima wallichii, S. argentea, Manglietia insignis, Magnolia championii,* and *Illicium yunnanense* (Fig. 21).

8. *Broad-leaved evergreen forests of the transitional tropical zone.* References: Chang et al. (1955); Ho and Chen (1963). These transitional forests occur at the boundaries between the subtropical and tropical zones. They are more or less similar in general appearance and structure to those of the tropical rain forests in containing mostly evergreen, broad-leaved trees with plank-buttress roots, stranglers, and cauliflory. However, in so far as dominance of trees is concerned, these forests are similar to the broad-leaved evergreen forests of the subtropics. The dominants are warm-loving trees of the Fagaceae, Lauraceae, Theaceae, Hamamelidaceae, and Elaeocarpaceae, which are mixed with some tropical trees belonging to the Euphorbiaceae, Melastomataceae, Proteaceae, Leguminosae, Moraceae, Myrtaceae, etc.

9. *Broad-leaved evergreen sclerophyllous woodlands or scrubs of the subtropical zone.* References: Editorial Board of Szechuan's Vegetation (1980). The distribution of such evergreen sclerophyllous woodlands is restricted mainly to the dry, sunny slopes on the mountains of the eastern Chinghai-Tibet Plateau at elevations ranging from 1,000 to 4,200 m. The climate is warm with a distinct dry season, and the annual precipitation is less than 1,000 mm. Under these climatic conditions, the dominant evergreen oaks have small, thickish, leathery, spiny leaves that prevent excessive transpiration. Thus, they form hard-leaved woodlands similar to those around the Mediterranean Sea. The oaks are *Quercus semecarpifolia, Q. aquifolioides, Q. spinosa, Q. longispica,* and *Q. senescens.* They can form forests, woodlands, or scrub in various habitats on the mountains; however, dwarf woodlands are commonly seen (Fig. 22).

10. *Bamboo evergreen forests of subtropical and tropical zones.* Reference: Editorial Board of Szechuan's Vegetation (1980). These bamboo forests are extensively distributed in subtropical and tropical China. There are many species of bamboos. Some bamboo forests are natural, but many are man-made. Different species adapt to different habitats. Species of *Sinarundinaria* are usually found naturally at high elevations in the mountains. Because bamboo stems have many uses, many species are widely cultivated in the subtropics. Among them, *Phyllostachys pubescens,* the young shoots of which are edible, is more commonly planted on acid soils, whereas *Sinocalmus affinis* is grown on calcareous soil. On marshy soils near river banks, *Phyllostachys congesta* is frequently encountered.

11. *Tropical broad-leaved semi-evergreen forests (tropical semi-evergreen seasonal forests).* References: Chang et al. (1955); Hou and Chu (1955); Kwangtung Institute of Botany (1976); Li (1956); Li et al. (1964). These forests are very similar in structure and appearance to tropical rain forests, but as the dry season becomes more distinct they merge into another type. Because the dominant trees are partly evergreen and partly deciduous, these forests are known as "semi-evergreen forests." This type differs from the tropical rain forests in several characteristics. The trees of the upper layer are lower and very few of the larger trees are buttressed. Furthermore, lianas and epiphytes are noticeably scarcer than in the tropical rain forest.

These forests can be classified into two groups. One group growing on limestone soils is widespread throughout southwestern Kwangsi and southern Yunnan provinces. It is composed of calcium-loving trees, such as *Ulmus lanciifolia, Gironniera nitida, Celtis austro-sinensis* (Ulma-

FIGURE 21. (Upper) Broad-leaved evergreen forest found on the acid soil in the subtropical region is dominated by evergreen oaks, consisting of *Castanopsis*, *Lithocarpus*, *Cyclobalanopsis*, and of *Schima superba* (with white-colored flowers).

FIGURE 22. (Lower) On the lee side of wet wind in the mountains of western Szechuan Basin, sclerophyllous woodland dominated by *Quercus aquifolioides* is found.

ceae), *Colona sinica, Burretiodendron hsienmu* (Tiliaceae), *Pometia tomentosa, Pseudonephelium confine, Delavaya yunnanensis* (Sapindaceae), *Muricococcum sinense, Drypetes perreticulata, D. confertiflorum* (Euphorbiaceae), *Garcinia tinctoria, G. paucinervis* (Guttiferae), *Caesalpinia sepiaria* (Leguminosae), etc. The second group is found on acid soils, mainly on western Hainan Island. It consists of trees such as *Kleinhovia hospita, Pterospermum heterophyllum, Heritiera angustata* (Sterculiaceae), *Chukrasia tabularis, Walsura cochinchinensis* (Meliaceae), *Spondia spinnata, Lannea grandis* (Anacardiaceae), *Antiaris toxicaria* (Moraceae), *Hainania trechosperma,* and *Microcos paniculata* (Tiliaceae).

12. *Tropical broad-leaved evergreen rain forests.* Reference: Kwangtung Institute of Botany (1976). Tropical rain forests are found locally on the eastern sides of Hainan and Taiwan Islands and in southern Yunnan Province where the local climate is saturated with moisture throughout the year. The forests are characterized by numerous species of evergreen trees. Giant trees, usually clothed with ferns, mosses, and epiphytes belonging to Orchidaceae and Araceae, reach a height of more than 30 m or more and often exhibit plank-buttresses and cauliflory. Stranglers are also characteristic.

These tropical rain forests are remarkable in their floristic richness. There are many trees belonging to the Lauraceae, Euphorbiaceae, Moraceae, Myrtaceae, Annonaceae, Apocynaceae, Sterculiaceae, Sapotaceae, Palmae, Rubiaceae, Myrsinaceae, Leguminosae, Dipterocarpaceae, Meliaceae, Sapindaceae, Aquifoliaceae, Theaceae, Rutaceae, Fagaceae, Proteaceae, and Samydaceae (Flacourtiaceae).

Some represenative species found in tropical rain forests in different localities are: *Vatica astrotricha, Amesiodendron chinense,* and *Tarrietia parvifolia,* in southern Hainan; *Dipterocarpus yunnanensis, Crypteronia paniculata, Pometia tomentosa, Terminalia myriocarpus,* and *Erythrina lithosperma,* in southern Yunnan; and *Myristica cagayanensis, Pterospermum niveum, Sideroxylon duclitan,* and *Artocarpus lanceolata,* in southeastern Taiwan (Fig. 23).

SCRUB AND COPPICEWOODS

1. *Broad-leaved deciduous scrub of the temperate zone.* Reference: Chen (1958). Leaf-shedding by shrubs of the temperate zone in northern and northwestern China is an adaptation to a cold season. The broad-leaved deciduous scrub is actually composed of two groups. One consists of primary vegetation that occurs on semi-arid sand dunes, with species of *Caragana, Salix,* and *Artemisia,* and on arid saline meadow soil mainly with species of *Tamarix.* The second, consisting of secondary vegetation formed after the felling of temperate forests, includes northern and southern scrubs. The northern temperate shrubs are dominated by *Corylus heterophylla, Lespedeza bicolor,* and coppicewood of *Quercus mongolica,* whereas the southern temperate shrubs are dominated by *Vitex negundo, Zizyphus jujuba, Cotinus coggygria* var. *cinerea, Coriaria sinica, Dalbergia hupeana,* and *Platycarya strobilacea* (Fig. 24).

2. *Mixed broad-leaved evergreen and deciduous scrub on acid soils of subtropical and tropical zones.* Reference: Hou (1951). Scrub growing on acid soils is all secondary, replacing subtropical and tropical forests after felling or fires, and is characterized by sunny and acid-loving plants. In the subtropical zone, scrub vegetation is dominated by shrubs belonging to the Ericaceae, Theaceae, Hamamelidaceae, and Fagaceae. *Rhododendron simsii, R. decorum, Vaccinium bracteatum, V. fragile, Eurya nitida, Ternstroemia gymnanthera, Loropetalum chinense,* and coppices of *Quercus fabri, Q. variabilis, Q. acutissima,* and *Castanea sequinii* are representative species. In the tropical zone, shrubs mostly belong to the Myrtaceae, Euphorbiaceae, Hypericaceae, Sterculiaceae, Rubiaceae, Theaceae, Rosaceae, etc. Representative species are *Rhodomyrtus tomentosa, Beackea frutescens. Melastoma candidum, M. normale, Aporosa chinensis, A. yunnanensis, Schima villosa, S. wallichii, Phyllanthus embrica,* and *Psychotria rubra.*

3. *Mixed broad-leaved evergreen and deciduous thorny scrub on limestone soils of subtropical and tropical zones.* Reference: Hou (1951). This scrub forms successional communities in limestone regions in subtropical and tropical zones. Calcareous limestone soil is excessively drained due to sinkholes, and therefore has low water-holding capacity. The shrubs on these soils exhibit greater defoliation and a marked calcicolous and xerophilous character and are thornier and/or more succulent in response to the dryness and high lime content of the soil.

In the subtropical zone, the plants belong to the Rosaceae, Rutaceae, Caprifoliaceae, Berber-

FIGURE 23. During the dry season in Yunnan Province, because of the presence of clouds that compensate for a shortage of rainfall in the winter, tropical rain forest is found locally in the valley. The tree is *Antiaris toxicaria* (Moraceae).

idaceae, Anacardiaceae, Rhamnaceae, Leguminosae, Euphorbiaceae, Ulmaceae, Meliaceae, Juglandaceae, etc. Typical genera are *Rosa, Rubus, Zanthoxylum, Berberis, Rhamnus, Viburnum,* and typical species include *Nandina domestica, Loropetalum chinense, Phyllanthus reticulatus, Prinsepia utilis,* and *Platycarya strobilacea.* In addition to the above-mentioned families, shrubs occurring in the tropical zone also consist of plants belonging to the Moraceae, Urticaceae, Sapotaceae, Sterculiaceae, Apocynaceae, Flacourtiaceae, Sapindaceae, etc. The

representative species include coppices of *Ficus* spp., *Alchornea trewioides, Boehmeria nivea, Clausena excavata, Sapium rotundifolium, Sterculia lanceolata, Desmos cochinchinensis, Pleomele nepalensis, Pterospermum heterophyllum, Terminalia hainanensis,* and *Wrightia hainanensis.*

4. *Broad evergreen sclerophyllous forests or scrub (mangrove) of the littoral subtropical and tropical zones.* Reference: Kwangtung Institute of Botany (1976). Along tropical and subtropical coasts of southern China, mangrove forests or scrub are distributed in muddy tidal marshes of estuaries. The best-developed mangrove forests, which can reach 10 to 15 m and have climbers, are found in the eastern part of Hainan Island at about 19°N. With increasing latitude, the number of species decreases until one species, *Avicennia marina,* remains. It occurs as 1 to 2 m-high shrubs at 27°N in North Fukien Province.

The evergreen leaves of mangroves possess a marked xerophilous structure and succulent character adapted to soil salinity. The chief mangrove genera are *Rhizophora, Bruguiera,* and *Ceriops.* They have viviparous seedlings and stilt roots or pneumatophores.

On the northern coast of the transitional tropics occur only five species, namely *Avicennia marina, Acanthus ilicifolius, Kandelia candel, Bruguiera conjugata, Aegiceras corniculatum,* which form shrubs less than 3 m tall. On the southern coast of Hainan Island more species of mangrove are present, namely, *Rhizophora apiculata, R. mucronata, Ceriops tagal, Bruguiera sexangula, B. cylindrica, Myoporum bontioides, Lumnitzera racemosa, Excoecaria agallocha, Hibiscus tiliaceus, Sonneratia caseolaris, Xylocarpus granatum, Scyphiphora hydrophyllacea,* and *Heritiera littoralis.* These mangrove species can reach 10 to 15 m, but are usually 5 m tall, and can include some climbers, namely *Dischidia chinensis, Derris trifoliata, Caesalpinia nuga,* and *Stenochlaena ilicifolius* (Fig. 25).

5. *Broad-leaved evergreen succulent scrub on coral islands of the tropical zone.* Reference: Chang (1974). In the South Sea of China are numerous coral islands where evaporation is greater than precipitation because of strong winds throughout the year. Shrubs 2 to 5 m tall growing on coral limestone soil along sandy beaches are evergreen and have succulent leaves and stems or leathery leaves that decrease the rate of transpiration. The vegetation is poor in floristic composition. Plants with thick succulent leaves are namely *Scaevola frutescens, S. hainanensis, Messerschmidia argentea, Guettarda speciosa, Morinda citrifolia,* and *Premna integrifolia.* A 5 to 8 m tall woodland dominated by *Pisonia grandis* is found in the center of the coral islands.

6. *Broad-leaved evergreen semi-sclerophyllous thickets (shrublands) on the mountains of temperate and subtropical zones.* Reference: Zhuo (1975). Areas dominated by semi-sclerophyllous *Rhododendron* species are commonly distributed beyond the limits of arborescent growth in the eastern Chinghai-Tibet plateau in alpine regions from 3,200 to 5,000 m in elevation. Typically, these communities are dense and are composed of dwarf, evergreen shrubs 2 to 15 dm tall. The shrubs are usually creeping, and their leaves are often leathery, thus reducing transpiration. *Rhododendron* species mixed with *Sinarundinaria* are frequently seen in the subalpine belt where they are always secondary after the felling of subalpine conifers. In some places deciduous shrubs, such as species of *Salix, Potentilla,* and *Caragana,* are also associated.

7. *Broad-leaved deciduous thickets (alpine shrublands) on the high mountains of temperate and subtropical zones.* Reference: Chang and Wang (1966). Alpine broad-leaved deciduous shrublands are distributed on the mountains of the eastern Chinghai-Tibet Plateau and in the northwestern high mountains. They usually are found on shady slopes in the high mountains beyond the limits of arborescent growth, whereas alpine meadows are seen on sunny slopes at the same elevation. The thickets are mainly composed of *Salix oritrepha, S. cupularis, Caragana jubata,* and *Potentilla fruticosa.*

8. *Tundras with evergreen dwarf-shrubs and mosses (mountain dwarf-shrub tundra) on high mountains in the temperate zones.* References: Chen et al. (1964); Chow and Li (1964). The mountain dwarf-shrub tundra is poorly developed on the summit of the temperate high mountains of the Changbaishan, Altai, and greater Khingan ranges. The soil is acid, and the climate is characterized by high humidity, strong winds, a short growing season, and local permafrost. The vegetation consists of dense growths of evergreen dwarf shrubs, mainly belonging to the Ericaceae, about 10 to 20 cm high and with small and tough leaves. Representative species are *Vaccinium vitis-idaea, Rhododendron aureum, R. confertissimum, R. redowskianum, Phyllodoce caerulea, Arctous japonicus, Empetrum sibiricum,* and deciduous dwarf shrubs such as

FIGURE 24. (Upper) Broad-leaved deciduous scrub is the secondary growth of the warm-temperate forest. *Cotinus coggygria* var. *cinerea* occurs on the shady slopes, whereas *Zizyphus jujuba* is found on sunny slopes.

FIGURE 25. (Lower) The best-developed mangrove, with 16 or 17 species, is encountered in the eastern part of Hainan Island. The mangrove trees or shrubs have stilt roots.

Arctous ruber, Salix rotundifolia, S. polyadenia, Betula rotundifolia, and mosses and lichens (Fig. 26).

9. *Alpine deciduous cushion sub-shrubs mixed with herbs of temperate and subtropical zones.* Reference: Chang and Wang (1966). The cushion sub-shrubs occur principally on the summits of mountains on the northwestern Chinghai-Tibet Plateau from 4,800 to 5,200 m in elevation. The plants assume the form of creeping dwarf sub-shrubs 2 to 5 cm high with richly developed, branched, horizontal axes that spread over the ground. The branches of these cushion plants are so compacted together that they touch each other on all sides. The climatic conditions under which this vegetation type grows resembles those of the mountain dwarf-shrub tundra in coldness and strong wind. However, they differ from those in that the humidity and precipitation are much lower, and the soil is alkaline. Because of this, acid-loving, ericaceous plants are absent, and the floristic composition of this vegetation type is entirely different. The plants belong mostly to the Caryophyllaceae (*Arenaria musiformis, A. diapensoides*), Primulaceae (*Androsace tapete*), Leguminosae (*Caragana saja, Oxytropis* spp.), Compositae (*Saussurea involucrata*), Rosaceae (*Potentilla* spp.), as well as species of Cyperaceae and Gramineae.

DESERTS AND XEROPHYTIC SHRUBS

1. *Temperate deciduous dwarf semi-shrubby deserts.* Reference: Integrated Survey Team of Sinkiang and Institute of Botany, Academia Sinica (1978). These deserts are stony, hilly, or sandy-pebbly with an extremely arid climate, and occur in western China. Only a few low-growing xero-halophytic plants occur infrequently in the cracks of rocks and in erosion gullys. However, a vast area of hills and the gravelly piedmont is devoid of vegetation. The soil contains a certain amount of gypsum. Dominant plants are *Salsola passerina, Reaumuria soongarica, Sympegma regelii, Iljinia regelii, Anabasis salsa, A. brevifolia,* and *Nanophyton erinaceum.* All these species are xerophytic halophytes, and the first two are gypsum plants that contain 1–4% of sulfur (Fig. 27).

2. *Temperate dwarf hairy sub-shrub deserts with ephemeral forbs.* References: Integrated Survey Team of Sinkiang and Institute of Botany, Academia Sinica (1978); Li (1961). This type of desert is found on loess-like, salt-free soils. It occurs on the lower slopes of mountains in the Dsungaria Basin where, although the annual precipitation is not more than 200 mm, it is distributed evenly throughout the year. The vegetation is predominantly composed of hairy dwarf-shrubs, namely, *Artemesia kaschgarica, A. borotalensis,* and *A. terrae-albae,* as well as some ephemerals that develop in spring, when the soil is moist, but fade quickly with the coming of summer. The perennial ephemerals commonly seen are *Poa bulbosa* var. *vivipara* and *Carex physodes.* Annuals are *Trigonella arcuata, Meniocus linifolius, Tetracme quadricornis,* and *Lepidium perfoliatum,* as well as *Ferula* spp., which are occasionally encountered.

3. *Temperate succulent halophytic dwarf sub-shrub deserts.* References: Integrated Survey Team of Sinkiang and Institute of Botany, Academica Sinica (1978); Wang (1964). This type of desert is extensively distributed in arid regions on soils with brackish underground water close to the surface, in the lower reaches of rivers, in hollows, or around salt lakes. The soils often have salt crystallizing on the surface with 10 to 30% NaCl or Na_2SO_4. Halophytes, such as *Kalidium foliatum, K. cuspidatum, K. gracile, K. caspicum, Halostachys belangeriana, Halocnemum strobilaceum, Suaeda physophora, S. microphylla, Nitraria sibirica,* and *Lycium ruthenicum* are dominants. Annual succulent hydrohalophytes, namely, *Salicornia europaea* and *Suaeda salsa,* occur on rather moist saline soil.

4. *Temperate shrub and sub-shrub deserts.* References: Hwang et al. (1962); Integrated Survey Team of Sinkiang and Institute of Botany, Academia Sinica (1978). This type of desert is widespread on the sand dunes and piedmont plains in the arid region. In the eastern gravelly Gobi plains with about 200 mm annual precipitation, the predominant shrubs are *Caragana tibetica, Tetraena mongolica, Potaninia mongolica, Ceratoides latens,* and evergreen *Ammopiptanthus mongolicus.* On the sand dunes, which can retain larger amounts of water, *Artemisia sphaerocephala, A. ordosica, Oxytropis aciphylla, Caragana microphylla,* and *C. korshinskii* occur. In the extremely arid area of the western region, *Ephedra przewalskii, Zygophyllum xanthozylon, Z. kaschgaricum, Nitraria sphaerocarpa,* and *Calligonium roborowskii* are scarce on the piedmont plains along the channels of temporary streams that are fed by the sur-

FIGURE 26. (Upper) Mountain dwarf-shrub-tundra, dominated by *Vaccinium vitis-idaea, Rhododendron aureum,* and other species of Ericaceae, is seen above 2,000 m on the upper mountinas of Changpaishan in northeastern China, above the forests.

FIGURE 27. (Lower) Rocky or hilly desert lacking all vegetation, in the Turfan Basin where annual precipitation usually is less than 20 mm. However, in the oasis, grapes grow very well under irrigation.

rounding snow-covered, high mountains. The sandy Takla-Makan desert is essentially devoid of vegetation, but *Tamarix* spp. are sparsely distributed in the dune valleys (Figs. 28, 29, 30).

5. *Temperate semi-arboreal deserts (Saksaoul communities).* References: Hu (1963); Integrated Survey Team of Sinkiang and Institute of Botany, Academia Sinica (1978). *Haloxylon ammodendron* and *H. persicum* are characteristic plants growing on the sandy deserts. Originally, *H. ammodendron* was widely distributed in the arid region of China, but it is now scarce in the Darim Basin. This species is a halophyte and is always associated with numerous saline plants. It usually grows on the bottom of sand dunes with moist and slightly saline soil or on salty soil with ground water at a depth of 5 to 8 m, which can be reached by the roots of this plant. This low tree can attain a height of 5 to 7 m and form small woods. *Haloxylon persicum*, a non-saline plant, is confined to the slopes or ridges of stabilized or semi-stabilized sand dunes in the Dsungaria Basin, where annual precipitation is distributed evenly throughout the year. Its growth is dependent upon rainfall, but not ground water. It often grows together with *Calligonum leucocladum, Artemisia santolina,* and *A. terrae-albae*, as well as some spring ephemerals (Figs. 31, 32).

6. *Cold high-mountain deserts with creeping or matted dwarf sub-shrubs of the temperate zone (cold high-plateau deserts).* Reference: Integrated Survey team of Sinkiang and Institute of Botany, Academica Sinica (1978). The cold high-plateau deserts are situated in the northwestern part of the Chinghai-Tibet Plateau, ranging in elevation from 4,600 to 5,500 m. They are characterized by the most extreme type of climate. The annual mean temperature ranges from −8° to −10°C; only July has a positive mean (10°C). Daily temperature variations of as much as 60°C can occur, but the rainfall seldom exceeds 100 mm. The wind is strong throughout the year. The vegetation is extremely poor in floristic composition, and it is composed of creeping dwarf scrubs. The dominant plant is *Ceratoides compacta* (Chenopodiaceae), associated with *Pegaeophyton scapiflorum, Hedinia tibetica, Parrya exscapa* (Cruciferae), *Oxytropis poncinsii* (Leguminosae), *Ajania tibetica, A. scharnhorstii,* and *Saussuria glandulifera* (Compositae). They are all mostly 4 to 15 cm tall (Fig. 33).

7. *Tropical and subtropical succulent thorny shrubs.* Reference: Editorial Board of Szechuan's Vegetation (1980). This type of vegetation, which always forms a complex with savannas in subtropical and tropical China, is somewhat allied to the southern Asiatic deserts. Because the potential evaporation is much greater than the precipitation in places where this type of vegetation occurs, the vegetation consists of xerophytes and succulents that require a certain minimum amount of water uptake even in periods of drought. Therefore, under warm and dry climatic conditions, plants with succulent stems such as *Opuntia ficus-indica* and *Euphorbia royleana,* and those with succulent leaves such as *Aloe vera* var. *chinensis, Kalanchoe pinnata,* etc. predominate. Additional plants are *Zizyphus mauritiana, Z. montana, Acacia farnesiana, Campylotropis yunnanensis, C. muehleana, Pandus tectorius,* and *Phoenix hanceana,* which are shrubs that have small, hard leaves or are clothed with hairs or spinules that offer some protection from excessive transpiration.

STEPPES AND SAVANNAS

1. *Temperate forb-grass steppes (mesoxerophytic steppes or meadow steppes).* References: Li (1962); Zhu (1958). This type of steppe is found in the temperate zone under a semi-humid climate with an annual precipitation of 350 to 500 mm. It is composed mainly of mesoxerophytic and sod-forming rhizomatous grasses, and subordinate tussock grasses mixed with numerous mesophytic herbs. It also is frequently associated with mesoxerophytic shrubs. Dominants belong mainly to the Gramineae, Compositae, and Leguminosae, as well as the Rosaceae, Ranunculaceae, Liliaceae, Umbelliferae, Scrophulariaceae, Caryophyllaceae, Campanulaceae, etc. Representative dominant species are *Aneurolepidium chinense, Stipa baicalensis, Filifolium sibiricum,* etc., usually mixed with shrubs including *Prunus sibirica, Salix mongolicus,* and *Ulmus pumila* in the north. In the south are *Bothriochloa ischaemum* and *Themeda triandra* var. *japonica,* which are frequently associated with shrubs such as *Zizyphus sativa* var. *spinosus, Sophora viciifolia, Hippophae rhamnoides, Rosa hugonis,* and *Prinsepia uniflora* (Fig. 34).

2. *Temperate needlegrass steppes.* References: Li (1962); Wang (1963). This type of steppe is distributed in the semi-arid region of the Inner Mongolia Plateau and Loess Plateau where the

FIGURE 28. (Upper) *Zygophyllum, Calligonum, Nitraria,* are sparsely distributed on the piedmont plains in the channels of temporary runoff in the southern desert region.
FIGURE 29. (Lower) *Ephedra przewalskii* occurs on the piedmont plains in the desert region.

FIGURE 30. (Upper) The wandering sandy desert Takla-Makan is essentially devoid of vegetation, but *Tamarix* spp. can be found very infrequently in the dune hollows. This air photograph was taken at about 1,000 m above the ground.

FIGURE 31. (Lower) In the Soongaria Basin of the desert region, the growth of *Haloxylon persicum* is confined to the slopes or ridges of semi-stabilized or stabilized sand dunes.

FIGURE 32. *Haloxylon ammodendron* was originally widespread in the entire desert region that had a ground water table at a depth of 5 to 8 m, which can be reached by roots of the plant. It usually is found on moist and saline soil.

annual precipitation is 250 to 350 mm. The vegetation is principally composed of xerophytic tussock grasses, such as *Stipa grandis*, *S. krylovii*, *S. breviflora*, and *Cleistogenes squarrosa*, that possess very extensive, finely branched root systems and narrow leaves that regulate their transpiration by inrolling. On sandy soil, sub-shrubs, including *Artemisia frigida*, *Kochia prostrata*, and *Thymus serphyllum*, and spiny shrubs, consisting of *Caragana microphylla*, *C. stenophylla*, etc.,

FIGURE 33. (Upper) The high-cold desert occurring at 5,000 m elevation in the northwesternmost part of the Chinghai-Tibet Plateau has very few species of plants. The dominant plants are *Ceratoides compacta* and *Ajania tibetica*.

FIGURE 34. (Lower)Mesoxerophytic or meadow steppe is distributed on the North East Plain and the eastern part of the Inner Mongolia Plateau, areas having 350 to 450 mm of rainfall annually. The dominant grass is *Aneurolepidium chinense*, and forbs are numerous.

are frequently found. In mountains of the desert region, steppes dominated by *Stipa capillata, S. krylovii,* and *Festuca sulcata,* also occupy a vast area (Fig. 35).

3. *Temperate dwarf-shrub or sub-shrub needlegrass steppes (desert steppes or semi-deserts).* Reference: Li (1962). This type of steppe is a transitional one between desert and steppe, and occurs in the temperate zone in places where the annual precipitation varies from 150 to 250 mm, and where the winters are dry and cold. The vegetation consists mainly of xerophytic subshrubs and dwarf grasses about 10 to 20 cm high. The extremely xerophytic grasses most frequently encountered are *Stipa gobica, S. glareosa, S. klemenzii, S. breviflora,* and *Cleistogenes mutica.* The dwarf sub-shrubs include *Artemisia frigida, A. xerophytica, Ajania achilleoides, A. tricolia, A. fruticulosa, Ceratoides latens, Salsola passerina,* and *Anabasis brevifolia.* The xerophytic dwarf-shrubs are *Caragana stenophylla, Prunus mongolica, Calligonum mongolicum,* and *Reaumuria soongarica.* In addition, *Allium polyrrhizum* and *A. mongolicum* are characteristic herbs of this type of steppe (Fig. 36). This type of vegetation also is found on mountains of the arid region.

4. *Subtropical and tropical savannas.* References: Editorial Board of Szechuan's Vegetation (1980); Kwangtung Institute of Botany (1976). Savanna-like vegetation in China is confined to a limited part of the subtropics and tropics. Savannas can be defined as homogeneous vegetation, consisting mainly of warm-loving and mesoxerophytic tussock grasses with a more or less even scattering of tall and small, evergreen and deciduous trees and thorny scrubs. The dominant warm-loving grasses are *Heteropogon contortus, Cymbopogon distans,* etc. Savannas are locally encountered in two regions of China. One group is found in western Yunnan and western Szechuan in the subtropical zone in deep valleys of the Hungtuan Mountains with locally dry and hot climate. There, the grasses are associated with *Zizyphus mauritiana, Acacia farnesiana,* and *Bauhinia racemosa.* Another group is distributed on the sandy, tropical coasts of Hainan and Taiwan islands where the grasses occur mixed with *Flacourtia indica, Pandanus tectorius, Albizzia procera,* and *Phoenix hanceana* (Fig. 37).

5. *High-mountain steppes of temperate and subtropical zones (cold high-mountain steppes).* References: Chang (1963); Wang and Li (1981). The major portion of western Chinghai and east central Chang Tang from 4,200 and 5,300 m above sea level in the Chinghai-Tibet Plateau is characterized by a continental type of climate with an annual precipitation of 200 to 300 mm. The annual mean temperature is below 0°C, and the wind is strong throughout the year. Low temperature is overcome during sunny weather by the intense insolation; thus daily temperature fluctuation is great. Under this dry and high-cold climate, the vegetation is composed mainly of cold-xerophytic, dense tussock grasses less than 20 cm tall and dwarf sub-shrubs with small, thick, hairy leaves. The dominants are *Stipa purpurea, S. subsessiliflora* var. *basiplumosa, Festuca olgae, Carex moorcroftii,* and *Artemisia wellbyi,* mixed with alpine elements such as *Kobresia* spp., *Thalictrum alpinum, Leontopodium alpinum,* and *Thermopsis alpina* (Fig. 38).

MEADOW AND SWAMP VEGETATION

1. *Temperate meadows.* References: Chen et al. (1954); Hou et al. (1953); Hou (1954); Wang and Li (1981). Most temperate meadows are not genuinely virginal, but, except for some saline meadows, are communities established under the disruptive influence of human activity and domestic animals. The plants of this vegetation type are mostly mesophytes, but the floristic composition varies with soils. On neutral or calcareous soils occur *Phragmites australis, Calamagrostic epigejos, Hemarthria compressa* var. *japonica, Deyeuxia langsdorffii, D. hirsuta,* and *D. angustifolia,* along with many species of forbs belonging to different families. However, there are numerous species of forbs, such as *Sanguisorba officinalis, Artemisia laciniata, Vicia* spp., and *Hemerocallis minor* associated locally with *Salix* spp. that grow on acid soils on sunny mountain slopes after the cutting of forests.

The floristic composition of halophytic meadows is entirely different from those mentioned above. This type of meadow is widespread in humid, semi-arid, and arid regions of the temperate zone in tidal estuaries along the coasts and inland salt marshes where many species of halophytic grasses and herbs are the same. They are *Aeluropus littoralis, Aneurolepidium dasystachys, Puccinellia distans, Scorzonera mongolica* var. *putjae, Xanthium sibiricum, Suaeda salsa, S. glauca, Atriplex littoralis, A. sibirica, Salicornia europaea, Limonium aureum, Polygonum*

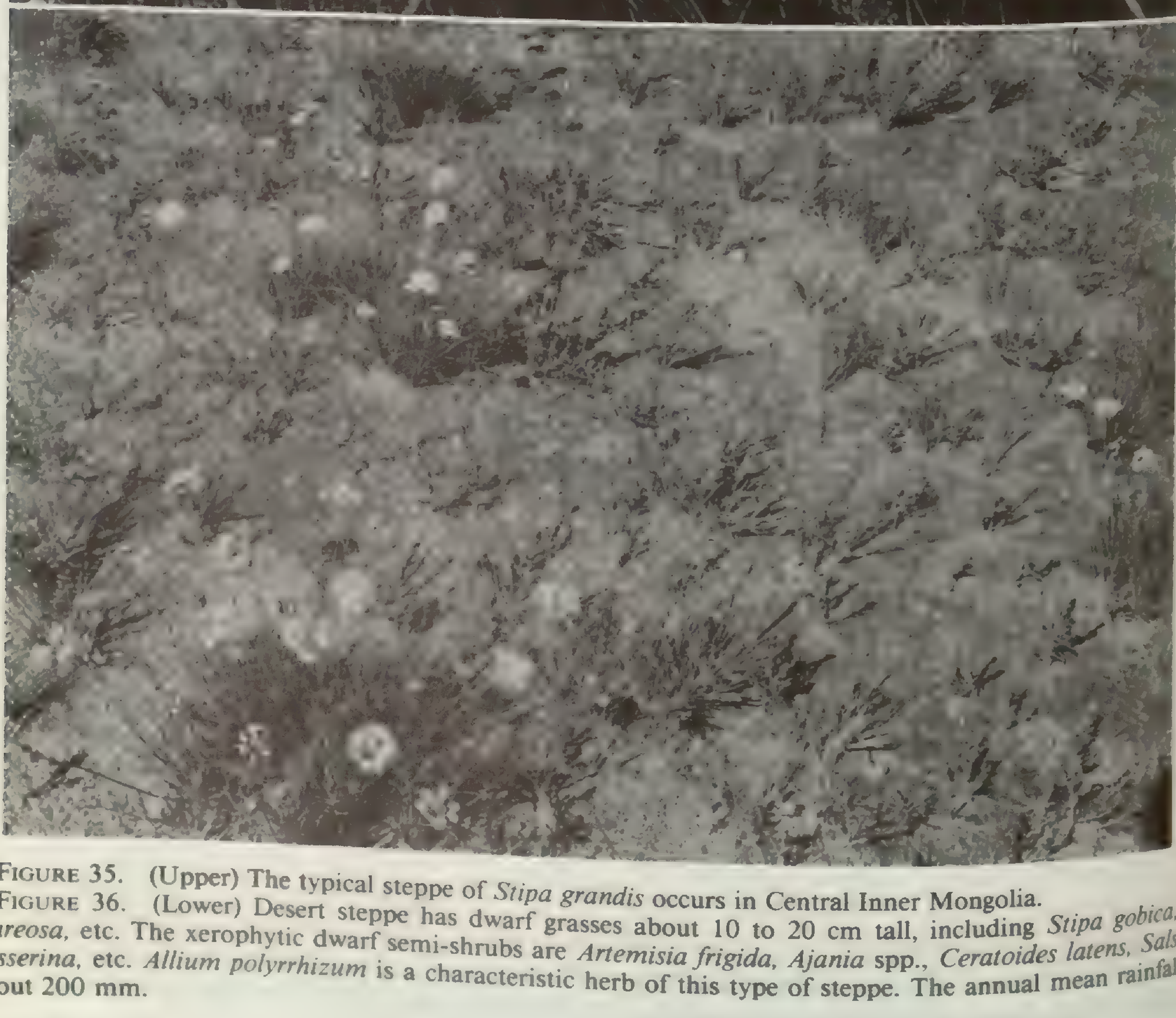

FIGURE 35. (Upper) The typical steppe of *Stipa grandis* occurs in Central Inner Mongolia.
FIGURE 36. (Lower) Desert steppe has dwarf grasses about 10 to 20 cm tall, including *Stipa gobica*, *S. glareosa*, etc. The xerophytic dwarf semi-shrubs are *Artemisia frigida*, *Ajania* spp., *Ceratoides latens*, *Salsola passerina*, etc. *Allium polyrrhizum* is a characteristic herb of this type of steppe. The annual mean rainfall is about 200 mm.

FIGURE 37. (Upper) On the lower slopes on the lee side of the Hengtuan Mountains in western Szechuan and Yunnan provinces, subtropical savannas are found. The dominant grasses are *Heteropogon contortus*, *Cymbopogon distans* mixed with trees such as *Pinus yunnanensis*, *Zizyphus mauritiana* and *Acacia farnesiana*.
FIGURE 38. (Lower) Cold high-mountain steppe, occurring in the central part of the Chinghai-Tibet Plateau, is dominated by *Stipa purpurea* and *S. subsessiliflora* var. *plumosa*.

sibiricum, and *Triglochin maritimum*. *Achnantherum splendens*, *Karelinia caspica*, and *Alhagi pseudalhagi* are confined to the arid region. However, the associated halophytic shrubs and sub-shrubs differ in these three regions with varying moisture conditions.

2. *Cold high-mountain meadows of temperate and subtropical zones.* References: Chen (1966); Kiang (1964). These meadows are essentially natural communities. They are distributed extensively in the high mountains of the Chinghai-Tibet Plateau beyond the limit of tree growth at elevations from 4,000 to 5,200 m and with an annual precipitation of 350 to 500 mm. They are mainly composed of numerous species of *Kobresia*, such as *K. pygmaea*, *K. tibetica*, *K. royleana*, and *K. humilis* and many alpine forbs such as *Polygonum viviparum*, *Thalictrum alpinum*, *Pedicularis* spp., and some alpine species of grasses. Successional subalpine meadows rich in forbs and grasses, with a few species of *Kobresia*, follow deforestation of subalpine meadows (Fig. 39).

3. *Subtropical and tropical meadows.* Reference: Kwangtung Institute of Botany (1976). The meadow vegetation or mesophytic grassland of humid subtropical and tropical zones is, in general, not a climatic climax, but rather a seral stage of succession formed after the felling of the forests. However, it can gradually merge into forests with the invasion of arborescent forms. The grassy or herbaceous taxa are sensitive to the combined influence of soil acidity and air temperature. The taxa of meadows found on subtropical acid soils are typified by numerous graminoids, such as *Eulalia speciosa*, *E. pallens*, *Miscanthus floridulus*, *Capillipedium parviflorum*, *Rhynchospora rubra*, *Fimbristylis* spp., and are frequently mixed with or dominated by pure stands of evergreen *Dicranopteris dichotoma* mixed with *Lycopodium cernuum* and *L. clavatum*. The meadows also are frequently associated with shrubs belonging to the Theaceae, Ericaceae, etc. However, on tropical, deep, moist, acid soils occur *Apluda mutica*, *Eremochloa ciliaris*, *Ischaenum aristatum*, and *Perotis indica*, as well as *Themeda gigantea*, and *Saccharum arundinaceum*. Evergreen *Blechnum orientale* is frequently seen on open roadsides. The tropical acid meadows are usually composed of shrubs belonging to the Euphorbiaceae, Melastomataceae, etc.

On the calcium or limestone soils the graminoids are represented by *Sporobolus elongatus*, *Bothriochloa intermedia*, *Neyraudia reynandiana*, *Heteropogon contortus*, *Pogonatherum crinitum*, *Capillipedium parviflorum*, and *Arthraxon hispidus*. Sometimes they are dominated by pure stands of *Cyclosorus acuminatus*, with *Pteris vittata* in the cracks of limestone rocks. Nevertheless, *Chrysopogon aciculatus*, *Heteropogon contortus*, *Apluda mutica*, *Kyllinga brevifolia*, and *Scleria levis* can be considered representative species on tropical limestone soils.

On tropical, coastal, sandy saline soils, often affected by sea spray, the meadow vegetation consists of graminoids, including *Spinifex littoreus*, *Sporobolus virginicus*, *Perotis indica*, *Cyperus malaccensis* var. *brevifolius*, together with forbs such as *Ipomaea pes-caprae*, *Wedelia prostrata*, *Limonium sinense*, *Suaeda australis*, and shrubby *Vitex trifolia* var. *unifoliata* (Fig. 40).

4. *Swamp vegetation.* The term "swamp vegetation" is applied to a type developing on water-logged soil where the summer water level is close to the ground surface (Meadow of U.S. terminology). In China the floristic composition of swamp vegetation varies with climate and soils. Swamps can also be classified according to their occurrence in temperate, subtropical, tropical, and cold, high mountainous areas (Fig. 41). Under similar climatic conditions, they are differentiated by edaphic factors.

VEGETATIONAL REGIONS OF CHINA

The longitudinal zonation of vegetation in the temperate zone, which is closely related to the east-to-west variation in annual precipitation, is shown in Figure 42. In eastern and southeastern China, the different forest regions correspond to the latitudinal zonation from north to south (Fig. 43). In the mountainous areas of the country the zonation of the vegetation is vertical.

Based on the principles of vegetational zonation, the country can be divided into eight vegetational regions (Fig. 44). References: Hou (1960, 1961, 1964, 1981a, 1981b, 1982).

1. *Cold-temperate deciduous needle-leaved forest region.* This region occupies the extreme north of China, embracing a very small area of the northern Greater Kingan Mountains with an annual precipitation of 500 mm. The mean annual temperature is below 0°C, and the extreme minimum is −50°C. The forest consists predominantly of *Larix gmelini* on acid podzolic soils. Many cultivated crops and fruit trees do not ripen in this region; however, potatoes, spring barley, and cabbage grow well.

2. *Temperate deciduous broad-leaved forest*

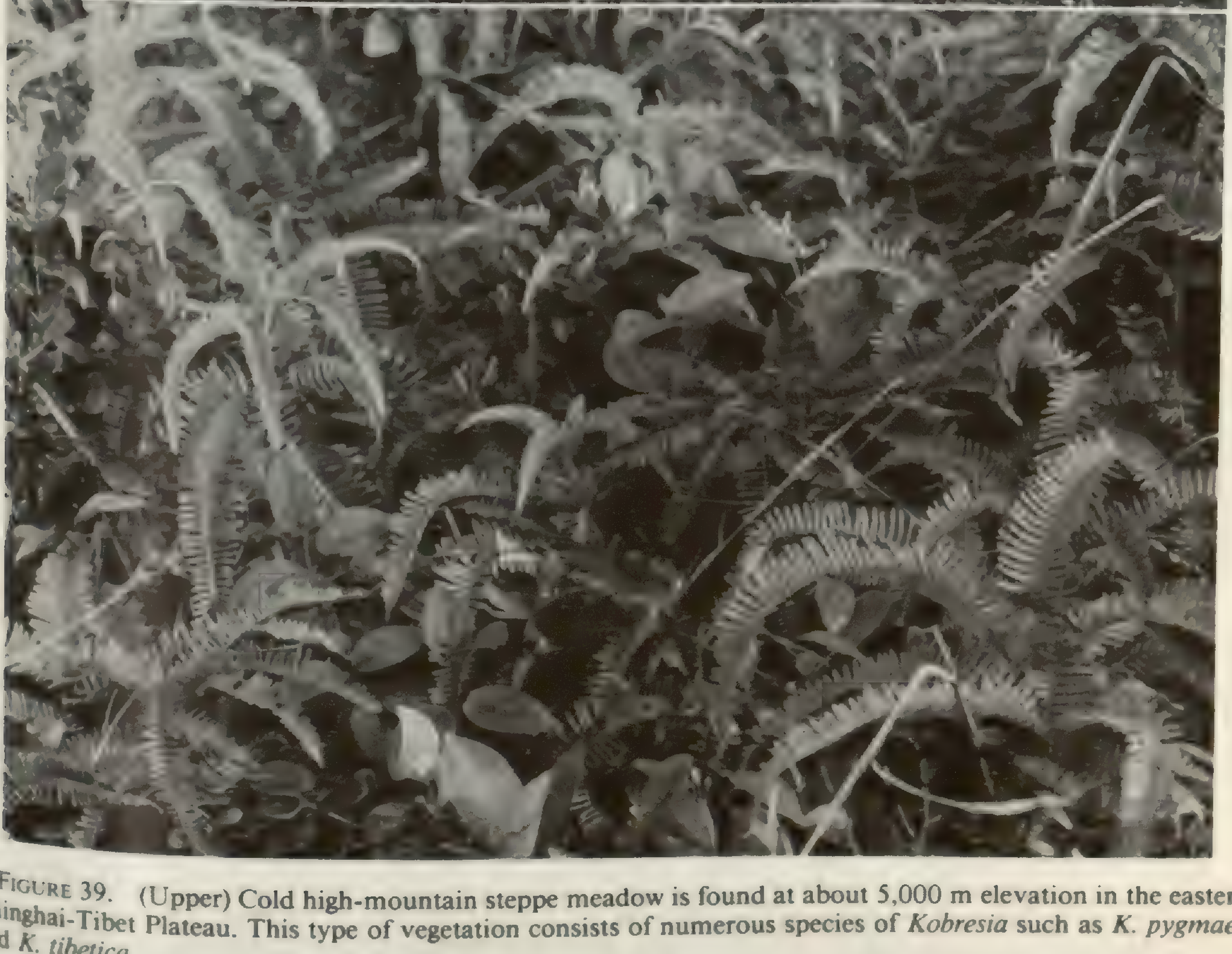

FIGURE 39. (Upper) Cold high-mountain steppe meadow is found at about 5,000 m elevation in the eastern Chinghai-Tibet Plateau. This type of vegetation consists of numerous species of *Kobresia* such as *K. pygmaea* and *K. tibetica*.

FIGURE 40. (Lower) *Dicranopteris dichotoma* is frequently encountered in the ground layer of *Pinus massoniana* woodland. In places, the fern forms pure stands. It, along with various associated plants, indicates strongly acid soil in the humid subtropics and tropics.

FIGURE 41. Swampy meadow of cold high-mountain at about 4,000 m elevation is frequently seen on the eastern Plateau.

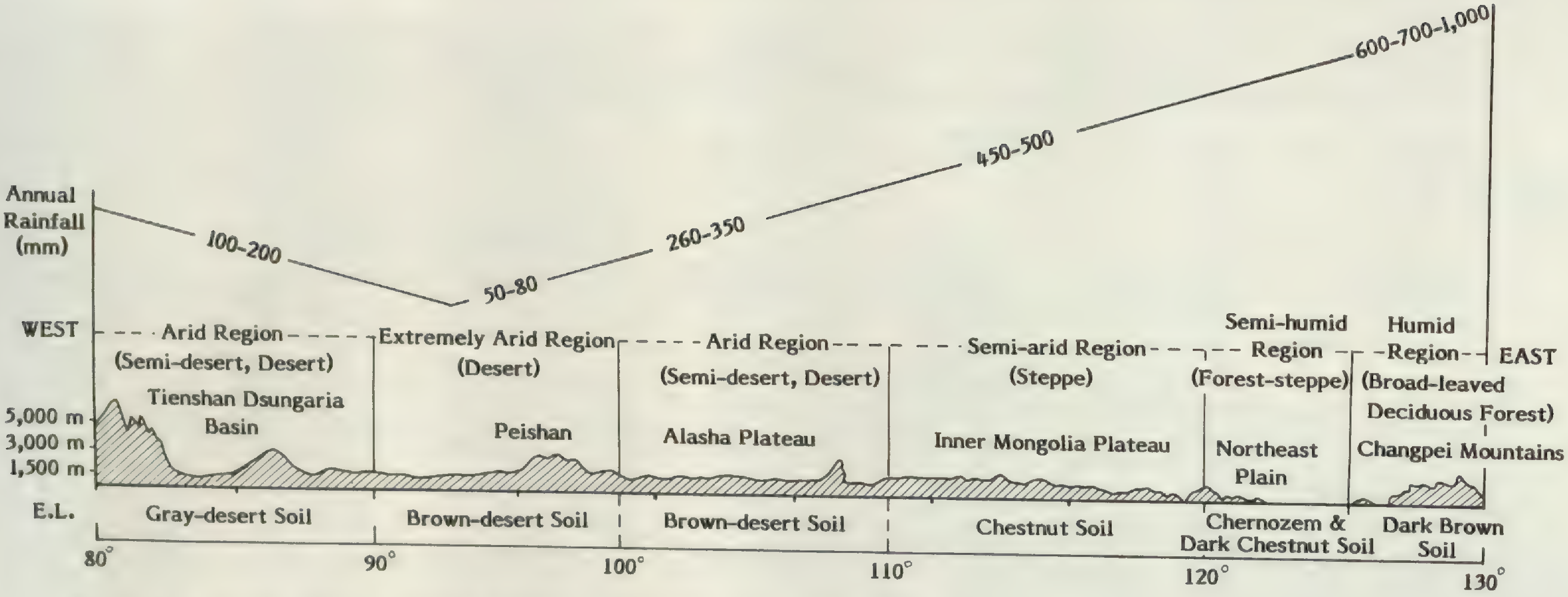

FIGURE 42. Schematic rainfall and soils in relation to vegetational regions varying from west to east in the temperate zone of China (about 42°N).

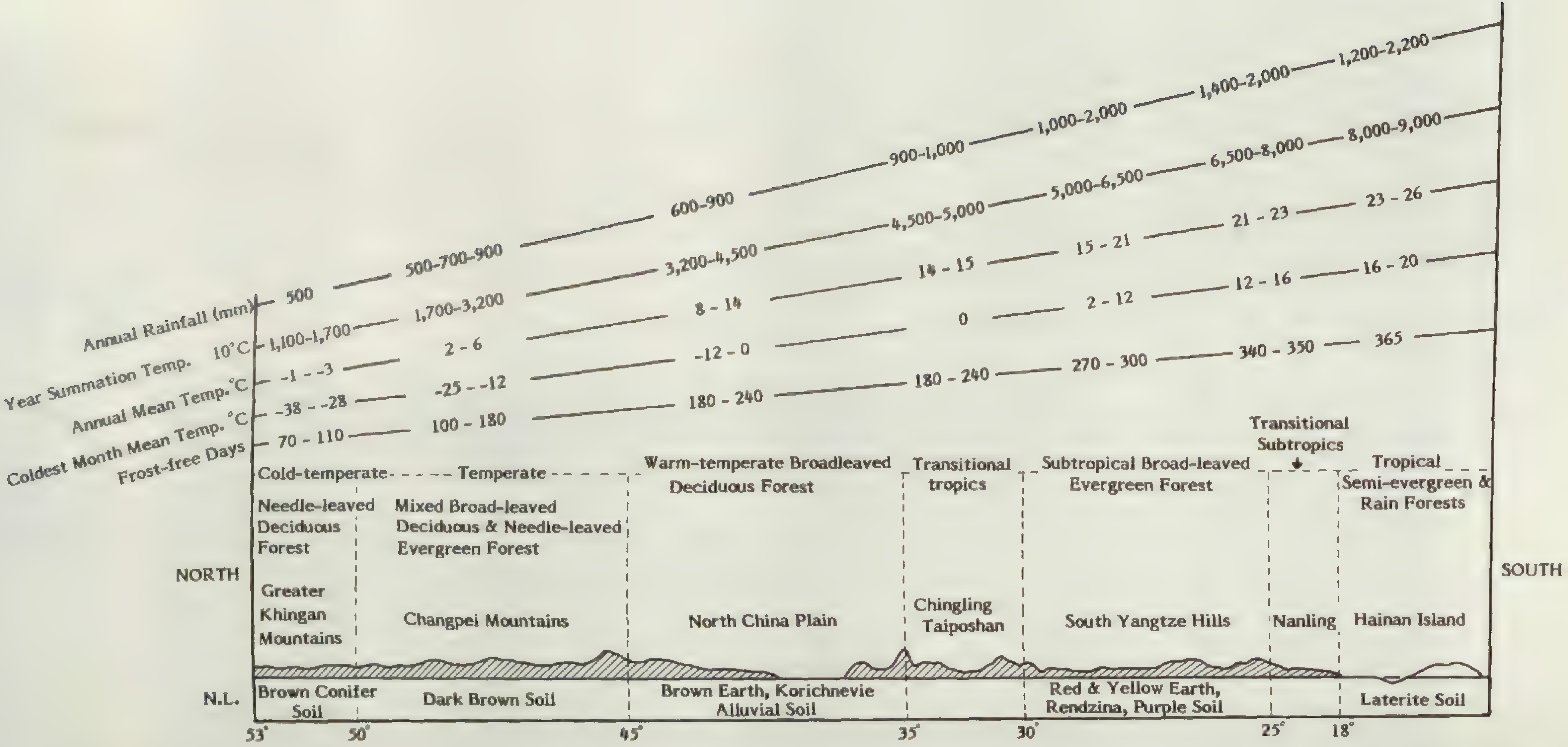

FIGURE 43. Schematic climate and soils in relation to vegetational regions varying from north to south in the eastern section of China (about 120° to 110°E).

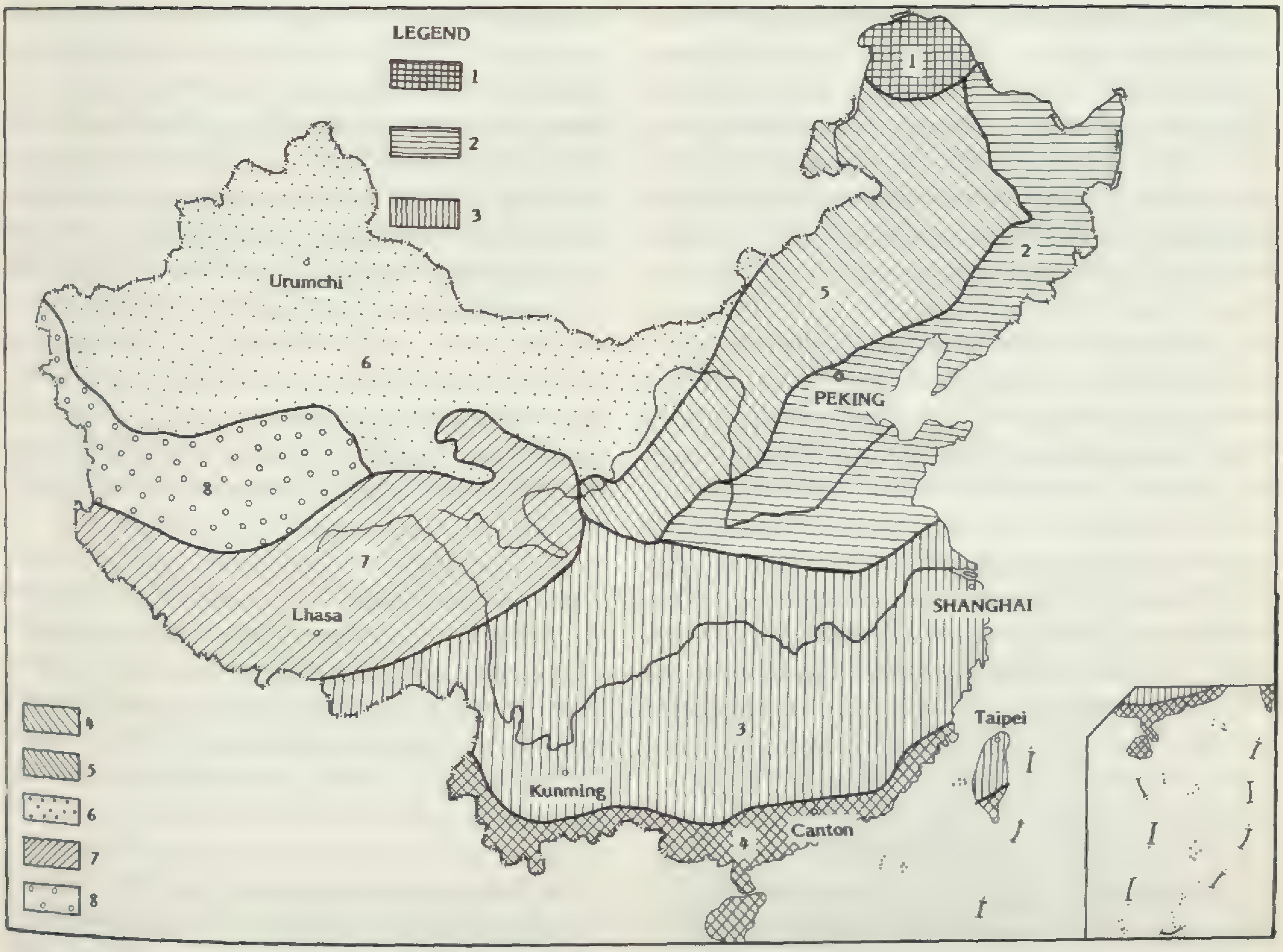

FIGURE 44. Map showing vegetational regions of China: 1) Cold-temperate deciduous needle-leaved forest region; 2) Temperate deciduous broad-leaved forest region; 3) Subtropical evergreen broad-leaved forest region; 4) Tropical seasonal rain forest region; 5) Temperate steppe region; 6) Temperate desert region; 7) High-cold meadow and steppe region; 8) High-cold semi-desert and desert region.

region. In this region the annual precipitation ranges from 600 to 900 mm. The northern part, with the mean annual temperature varying from 1° to 8°C, supports a mixed deciduous broad-leaved and evergreen needle-leaved forest. From the lowlands at about 300 m up to the highest peak of Changpaishan at 2,700 m, the following vegetation types appear in succession: *Quercus mongolica* forest; mixed *Pinus koraiensis*-deciduous broad-leaved forest; *Abies nephrolepis* and *Picea jezoensis* forest associated with a secondary forest dominated by *Betula platyphylla*; *Betula ermanii* forest; and the dwarf-shrub tundra. In the valleys and alluvial plains, soybeans, spring wheat, maize, kaoliang, millet, and rice are planted once a year.

The southern part of Region 2 principally covers the North China Plain, where the mean annual temperature varies from 8° to 14°C. The deciduous broad-leaved forest consists of *Quercus dentata, Q. liaotungensis, Q. aliena,* etc. Evergreen needle-leaved forest is dominated by *Pinus tabulaeformis* or *P. densiflora* and grows on acid, brown forest soil. Mixed deciduous broad-leaved forest and the *Platycladus orientalis* forest thrive on the neutral or calcareous Korichnevie soil. Saline meadows are widely distributed along the sea coast. The land is almost entirely under cultivation and usually is planted three times in two years with winter wheat, cotton, peanuts, sweet potatoes, maize, kaoliang, and millet. Rice is locally planted once a year.

Region 2 is the main production area in China of deciduous fruits, namely, apples, pears, grapes, persimmons, chestnuts, walnuts, and Chinese dates.

3. *Subtropical evergreen broad-leaved forest region.* Occupying a vast area of the southwestern and southeastern part of the country, this region is characterized by different types of subtropical forests. In the eastern subregion, the climate is moist and warm. The annual precipitation is 1,000 to 2,000 mm and the mean annual temperature varies from 16° to 20°C. The ever-

green broad-leaved forest, dominated by *Cyclobalanopsis glauca, Castanopsis eyrei, Lithocarpus glaber,* etc., the evergreen needle-leaved forest, dominated by *Pinus massoniana* and *Cunninghamia lanceolata,* and the *Phyllostachys pubescens* forest grow on acid, yellow or red, podzolic soils. On the limestone soils occur mixed deciduous and evergreen broad-leaved forests characterized by trees belonging to the Ulmaceae and some other calcium-loving families. There are also forests dominated by *Cupressus funebris, Sinocalmus affinis,* etc. The vertical distribution of the vegetation can be represented by the eastern slope of Erlanshan where evergreen broad-leaved forest, mixed evergreen and deciduous broad-leaved forest, *Abies fabri* forest, and *Sinarundinaria* scrub appear successively from the base to the 3,300 m top of the mountain.

In the western subregion where the climate is warm and rather dry with an annual precipitation less than 1,000 mm, sclerophyllous evergreen oak forest, dominated by *Quercus aquifolioides,* is found on the sunny slopes, and succulent thorn scrub dominated by *Opuntia ficus-indica* and *Euphorbia royleana* occurs in the deep, dry valleys. There the evergreen broad-leaved forest consists of *Cyclobalanopsis glaucoides, Castanopsis delavayi,* and *Lithocarpus dealbatus. Pinus yunnanensis, P. armandii,* and *Cupressus duclouxiana* are the dominant trees of the evergreen needle-leaved forest.

In the eastern subregion two crops consisting of summer rice and winter wheat or rapeseed are usually planted each year. Double-cropping of rice, followed by a planting of a cool-loving crop, also can occur. Cotton, ramie, peanuts, sweet potatoes, maize, and sugar cane are the common crops. Subtropical fruits such as *Citrus* spp., *Myrica rubra,* and other cultivated trees such as tea, tea oil, loquat, tung oil, and mulberry are widely grown. In the western subregion, however, summer rice or maize and winter wheat or rapeseed are planted annually, whereas the fruit trees are mainly deciduous.

4. *Tropical seasonal rain forest region.* This region lies in southernmost China where the annual mean temperature ranges from 21° to 26°C, and the precipitation is 1,200 to 2,200 mm annually. In well-sheltered valleys one can find thick, broad-leaved evergreen rain forest with a wide variety of trees of different heights, some up to 40 m. The massive trunks are supported by buttresses taller than a man and entwined with thick vines. Lovely ferns and brilliant orchids flourish on some of the trees. Tropical broad-leaved semi-evergreen forest (tropical seasonal forest) occurs on limestone hills or on drier sites. Along the sea coast, mangroves containing *Kandelia candel, Rhizophora mucronata, R. apiculata,* and *Bruguiera sexangula* are confined to saline, muddy, swampy soils. Some species produce a tangle of arching prop roots from their base, which enables them to stand up to strong wind and waves. Other species have air-roots with tiny holes that project above the mud and supply the submerged roots with air. A number of them produce viviparous seeds that germinate while still attached to the tree. When these sprouted seeds drop, they readily take root in the shifting mud.

In this region rice frequently yields two crops a year. Sweet potatoes, maize, and peanuts can be raised in the winter. Also cultivated are evergreen orchards of tropical fruits, bananas, pineapples, lichees, longans, mangoes, and betelnuts, as well as plantations of industrial crops such as rubber, coconut, coffee, pepper, vanilla, and oil palm in the southernmost part. There are also fields of sugar cane, manioc, and sisal hemp.

5. *Temperate steppe region.* The plain of China's northeast and the eastern portion of the Inner Mongolia Plateau is a vast grassland with a semi-arid climate. The eastern part is covered with a mesoxerophytic steppe and meadows dominated by *Aneurolepidium chinense* and *Filifolium sibiricum* that grow on loamy chernozem or dark chestnut soils. Sparse mesoxerophytic woodland dominated by *Pinus sylvestris* var. *mongolica* or *Ulmus pumila* is found on sandy soils. Typical steppe occurs in the western parts of the Inner Mongolian and Loess plateaus, where the xerophytic perennial grasses, *Stipa grandis, S. krylovii, S. bungeana, S. brevifolia, S. gobica, S. glareosa,* and *Cleistogenes squarrosa* are dominant. The deciduous scrub, including *Salix* spp., *Caragana* spp., and *Artemisia* spp., grows on the sandy soil or sand dunes of this region. Saline meadows and the annual succulent halophytic vegetation frequently occur on soils with high ground-water tables. Grasses and leguminous forage plants in this area are highly nutritional, making the region China's main livestock-raising area. The main domestic animals here are sheep, cattle, and horses.

A number of places in the eastern part of this region have been turned into agricultural areas with state farms raising crops and breeding stock. Their main crops are soy beans, sorghum, and sugar beets.

6. *Temperate desert region.* This region includes the western parts of Inner Mongolia, Kansu, the Tsaidam Basin in Chinghai Province, and the whole of Sinkiang. The characteristic feature of the climate is its dryness; the annual mean precipitation is less than 50 to 150 mm in most places. The sandy deserts and areas of gravelly gobi contain a poor variety of plants. Growth is sparse, and there are stretches that are devoid of vegetation.

Among the few plants that grow in the sandy deserts of this region are *Haloxylon ammodendron, H. persicum, Artemisia sphaerocephala, A. ordosica,* and *Calligonum* spp. On the gravelly gobi patches, *Ephedra przewalskii, Nitraria sphaerocarpa, Anabasis* spp., *Salsola passerina,* and *Reaumuria soongarica* occur. The succulent halophytic dwarf semi-shrubby desert dominated with *Kalidium* spp., *Nitraria sibirica, Halostachys belangeriana,* and *Halocnemum strobilaceum* is confined to solonchak soil. *Sympegma regelii* grows very sparsely in the rocky desert. Most of the above-mentioned plants make excellent camel fodder. The leaves of some of these plants are vestigial, their function having been taken over by green branches to reduce transpiration.

In the temperate desert region *Populus euphratica* woodland, sometimes with *Elaeagnus angustifolia,* is found on river banks. The leaves of *Populus* make an excellent fodder for camels and goats. This tree is the main source of timber in the desert. *Tamarix* scrub occurs on saline meadow soils with a high water table.

The vast grasslands on the slopes of the high mountains in the Chilien, Tienshan, Kunlung, and Altai ranges are good grazing grounds. There are timber forests consisting mostly of *Picea* spp. on the upper slopes. The melting of the perpetual ice and snow on the peaks irrigates the oases in the deserts below. The low-elevation basins in this region are centers for growing fruit, such as grapes, watermelons, and Hami melons. Because the strong sunlight and the great fluctuation of temperatures between day and night are favorable for concentrating sugar, the fruits are extraordinarily sweet. In addition, China's best long-staple cotton is grown in the Turfan Basin.

7. *High-cold meadow and steppe region.* The eastcentral and southern portions of the Chinghai-Tibet Plateau are 4,000 m above sea level and have no summer. The melting glaciers produce many marshes, lakes, and meadows with *Kobresia pygmaea, K. tibetica,* etc. The high-mountain alpine steppe occurs in the central part and is dominated by *Stipa purpurea* and *S. subsessiliflora* var. *basiplumosa.* Yaks, Tibetan goats, and sheep are the main domestic animals there. In the valleys of the plateau grow such cold-resistant crops as rapeseed, spring barley, turnips, etc. They are locally seen at elevations below 3,200 m in the north and 4,200 m in the south.

8. *High-cold semi-desert and desert region.* The northwestern corner of Tibet, at 5,000 m above sea level, has even sparser vegetation and fewer varieties of plants. Only short, small sub-shrubs are found here. Some of these are creepers, whereas others are cushion plants, forms that are adapted to resisting wind and cold and preserving moisture. *Ceratoides compacta* and *Ajania tibetica* are frequently found on the sandy gravelly desert. There is no agriculture in this region.

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QUATERNARY HISTORY OF DECIDUOUS FORESTS OF EASTERN NORTH AMERICA AND EUROPE[1]

MARGARET B. DAVIS[2]

ABSTRACT

The temperate deciduous forest of North America is more diverse than the deciduous forest of western Europe. This difference has traditionally been explained by greater survival in North America of deciduous species during the Quaternary. More recent investigations have shown, however, that late-Tertiary forests of Europe had already become dominated by conifers, with deciduous angiosperms a minor component. During the Quaternary, coniferous species and genera were lost from the European flora, leaving a few species and genera of angiosperms as the dominant trees. Cold, dry, continental climate during the glaciations caused the extinction of conifers; deciduous trees apparently survived these climatic conditions in pockets of favorable habitat in the eastern Mediterranean region. In eastern North America, in contrast, temperate deciduous forests are quite similar to the forests that were present in the late Tertiary. During the Quaternary, relatively few extinctions occurred, although deciduous angiosperms were displaced from the Appalachian mountains, surviving in small populations in the lower Mississippi valley or on the southern coastal plain. Coniferous forests dominated by spruce grew in the Great Plains, and forests dominated by pine grew on the southern part of the Atlantic coastal plain. At the opening of the Holocene, and presumably at the beginning of all the previous interglacials, tree distributions changed dramatically as temperate species rapidly extended their ranges northward. Range boundaries have continued to change throughout the Holocene, as expansions and contractions of range have occurred as the result of climatic change. Quaternary climatic history caused dramatic changes in the forests of both areas, indicating that modern species distributions can no longer be considered relicts of Tertiary distributions. Throughout the Quaternary, species ranges have changed in response to changes in regional climate; many forest communities are of recent origin, having received their present complements of tree species within the last 5,000 years. Forest communities in Eastern North America and in Western Europe as well have been invaded repeatedly during the Holocene by forest species expanding from refuges far to the south.

Temperate deciduous forest grows over a wide area of eastern North America. The forest is rich in numbers of species, especially the mixed mesophytic forest communities of the southern Appalachians. These forests were traditionally compared with forests of the Tertiary Period (Reid, 1935; Braun, 1947, 1950; Campbell, 1982), when the so-called Arcto-Tertiary geoflora was supposed to have been widespread throughout the northern hemisphere (Chaney, 1944). Reid (1935) and Chaney (1944) believed that severe climate during the Quaternary Period eliminated the Arcto-Tertiary geoflora entirely from many regions, such as western North America, while in others, such as western Europe, extinctions eliminated all but a few species and genera. The modern deciduous forests were thus seen as remnants of an originally widespread, uniform vegetation.

The geoflora concept has been challenged recently by Wolfe (1978, 1979) who argued that a uniform broad-leaved forest never existed. His analysis of the paleobotanical data shows that Tertiary floras were diverse, with evergreen gymnosperms such as *Sequoia* dominant in some regions, and evergreen angiosperms present elsewhere. He argued that a number of major climatic changes occurred during the Tertiary, especially during the Oligocene; these changes led to local changes in abundances of various components of the Tertiary flora. Thus changes of climate caused local adaptations rather than migrations of intact plant communities from one latitude to another as Chaney hypothesized (Wolfe, 1979). Before the end of the Tertiary Period, the forests of western United States were already dominated by conifers. A similar change had also occurred in Europe, where Pliocene floras contained many genera and species of conifers (Wolfe, 1979). *Sequoia* was the dominant tree in some regions (Traverse, 1982).

Mixed coniferous-deciduous forest in Europe during the Pliocene is a new interpretation of forest history that stands in marked contrast to the traditional view. The traditional view held that deciduous forest persisted in Europe into the early Quaternary Period, when increasing se-

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verity of climate caused extinctions of many angiosperm trees (Tralau, 1973; Campbell, 1982). In contrast, Wolfe emphasized that coniferous species and genera were the important losses from the European flora during the Quaternary. The Taxodiaceae, for example, once so important in the Black Sea region, were eliminated entirely (Traverse, 1982). The angiospermous genera that remain today represent differential survival of one component of what had been mixed coniferous-deciduous forest (Wolfe, 1979). Wolfe pointed out that Europe today has the type of climatic regime that elsewhere in the world supports mixed coniferous forest; the dominance of deciduous species in the region today is therefore anomalous. Eastern North America, in contrast, has a climatic regime typical of deciduous forest regions. Today it supports forests dominated by deciduous angiosperms, just as it did during the late Tertiary (Wolfe, 1979).

The Quaternary pollen record adds a useful perspective to these differing views of the origin of the European deciduous forest and the relationship of deciduous forests in eastern North America and Europe. First, the Quaternary record shows that dramatic changes in the geographical ranges of forest species occurred during the Quaternary. We can no longer speak of Tertiary forest "remaining" in a region throughout the Quaternary, because many tree species were repeatedly displaced during the Quaternary from the geographical region where they now occur. For this reason, *modern geographical ranges cannot be used to identify the locations of "relict" Tertiary forests.* Second, the response of temperate forest trees to Quaternary climatic change was individualistic, supporting Wolfe's contention that *Tertiary floras would not have migrated as units in response to climatic events.* Third, the extinctions that occurred during the Quaternary, especially the differential extinctions of conifers and deciduous angiosperms document that *the differential severity of Quaternary climate affected forests differently in Europe and North America.* These three factors contributed to the makeup of the modern temperate forest floras of North America and Europe.

In considering how Quaternary climate changed Pliocene floras into modern floras, the two phases of Quaternary climate, glacial climates and interglacial climates, are important. The two phases appear to have had quite different effects. Glacial phases, i.e., times when ice sheets were more extensive than at present, comprised about 90 percent of the time during the Quaternary period. During these long, cold intervals, temperate species survived in small populations that were susceptible to extinction. The severity of the climate, both in terms of average temperature, continentality, and drought; the extent of geographical displacement of plant species; the sizes of populations; and the community composition of forests in refuge areas; all had an effect on the probability of extinction for individual species.

Interglacial intervals comprised a much smaller proportion (about 10 percent) of the Quaternary period. They were characterized by climates similar to those of today, which in Europe and eastern North America seem to bear a general resemblance to late-Tertiary climate. Each interglacial was short, lasting only 10,000 to 15,000 years, and began and ended with a sudden, major climatic change (Emiliani, 1972; Broecker & Van Donk, 1970). The interglacials, although favorable for survival and population expansion of temperate forest trees both in Europe and eastern North America, were times of vegetational instability. During interglacials the geographical distributions of temperate species shifted many hundreds of kilometers, and the composition of forest comunities changed rapidly.

Geological Evidence of Events During the Quaternary Period

The exploration of the deep sea by geologists in the last twenty years has led to a new understanding of Quaternary events, revolutionizing our thinking about the time scale of glaciation. Many marine cores include sediment extending through the entire Quaternary Period. Previously, four major glaciations were recognized within the Quaternary. We now know that there were 18 or 20 glaciations during the last 2 million years, the time interval now assigned to the Quaternary. Each of these glacial cycles lasted about 100,000 years (Hays et al., 1969). Figure 1 shows oxygen-isotope paleoclimatic records for the last 800,000 years. The climatic events are well dated: the last interglacial (the earliest part of stage 5) started 125,000 years ago, lasted about 15,000 years, and ended with a sharp decline in temperature that initiated the last glaciation. Warm conditions returned, followed by a cold period, then a short warm interval. Seventy thousand years ago a long cold interval (stages 2–4) began, which culminated in the glacial maximum 18,000 to 20,000 years ago (Broecker & Van Donk, 1970).

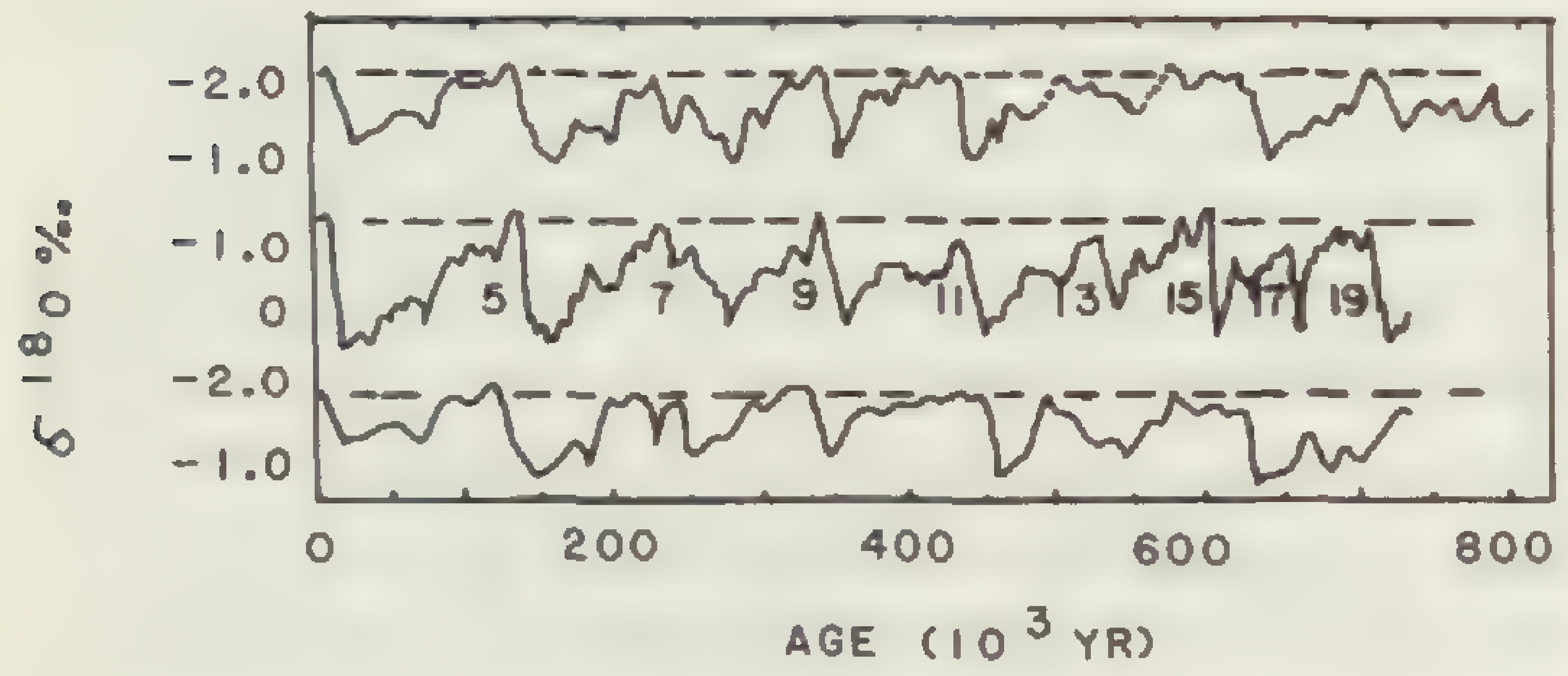

FIGURE 1. Oxygen-isotope ratios in three deep-sea cores, plotted against time. The low points on the curves represent periods when glaciers were expanded, the high points, periods when glaciers were contracted. Interglacial stages are indicated by Arabic numerals 5, 7, 9, etc., but glaciers were as small as today (isotope curves above dashed lines) for only short periods during the Quaternary. The three cores record nine glacial-interglacial cycles during the last 800,000 years (modified from Johnson, 1982).

A number of aspects of this record are important to vegetation history. The first is that changes occurred much more rapidly than previously supposed. We had imagined four rather leisurely glacial-interglacial cycles, each lasting several hundred thousand years, with long interglacials equal to, or longer than, glacial periods. The newer data indicate that interglacial periods were brief, 10,000 to 15,000 years in length, while the glacial intervals were much longer, lasting about 100,000 years. During glacial intervals there were fluctuations of climate culminating in a severe, but relatively brief glacial maximum and then a rapid, large temperature rise into the next interglacial (Broecker & Van Donk, 1970). The present interglacial, the Holocene, is typical in length for an interglacial, meaning that events recorded in Holocene sediments can be used as an analog for events during previous interglacials.

FULL-GLACIAL VEGETATION OF NORTH AMERICA

Cores of lake sediment have yielded detailed information about vegetation changes during the glacial-interglacial cycles. Sediments can be sampled at close intervals, a few hundred years or even decades apart, and pollen assemblages for the last 50,000 years can be dated by radiocarbon. Pollen percentage assemblages can be compared with assemblages in surface samples, collected from different vegetation regions. More than 1,800 surface samples are available for comparison from different parts of eastern United States and Canada (Overpeck & Webb, 1983). These can be compared with quantitative samples of modern forest to show how the percentages of pollen relate to the percentages of growth stock volume in the modern forest (Delcourt et al., 1983). In addition, pollen concentrations in sediment can be corrected for the rate at which the sediment matrix has accumulated, and thus the actual numbers of pollen grains deposited every year on the sediment surface can be determined (Davis & Deevey, 1964). Comparisons of modern pollen deposition rates and forest records show that pollen deposition is proportional to the density of source trees within a 15 km radius of the deposition site (Davis et al., 1973; Webb et al., 1981). Although imprecisions arise because pollen grains are produced in different amounts by different species and are transported different distances, we nevertheless can use pollen to obtain not only a list of the flora, but also roughly quantitative information about the abundances of different kinds of trees. Macrofossil studies are used increasingly in combination with pollen studies to provide species identifications and definitive proof of the local presence of particular plant species (e.g., Watts, 1979; Davis et al., 1980).

Eastern United States is shown in Figure 2, with black dots indicating sites where sediments are securely dated by radiocarbon at 18,000 to 20,000 years before present, when the ice stood at its maximum. Most of these sites have been studied within the last 15 years.

The new paleobotanical data demonstrate that the vegetation during the last glacial period was very different from modern vegetation (Watts, 1980, 1984). Furthermore, most of the plant communities were dissimilar from any plant communities that are widespread today. Contrary to previous thinking, the latitudinal zonation of modern forest communities was not merely displaced southward in response to displacement of climatic zones (Martin, 1958). Instead a very different series of vegetation types developed, without modern analogs. South of the glacial boundary in New York and in Pennsylvania there was a belt of tundra, which might have been 100 to 200 km wide, extending southward at high elevations along the mountains (Watts, 1979; Maxwell & Davis, 1972). Treeline was at about 1,000 m elevation in western Maryland (Watts, 1979).

Along the Atlantic coastal plain there was coniferous forest, with *Pinus, Picea, Abies,* and *Larix* (Watts, 1984; Whitehead, 1973, 1981). *Picea*

was common in the north, but farther south, it became quite rare and *Pinus* was dominant. The pollen assemblages from South Carolina leave it ambiguous whether there was dense forest or semi-open vegetation (Whitehead, 1973; Watts, 1983), but it is clear that deciduous trees were rare or absent. On the southern coastal plain and piedmont as far south as northern Florida, *Pinus* was the dominant tree (Watts, 1970, 1983; Watts & Stuiver, 1980). There were only trace quantities of deciduous tree pollen at sites north of northern Florida (Watts, 1970, 1980; Watts & Stuiver, 1980; Whitehead, 1973, 1981).

On the western flank of the Appalachians, *Pinus* pollen dominated the fossil assemblage (Delcourt, 1979). But in the Mississippi valley, *Picea* pollen was abundant, and *Pinus* pollen was absent (Delcourt et al., 1980). Farther north and west on the Great Plains, *Picea* and *Larix* were the dominant trees. *Pinus* was present before 24,000 years ago, but it became extinct just before the last glacial maximum. Unlike the modern boreal forest, which contains both *Pinus* and *Picea*, especially in the central part of Canada, *Picea* dominated the full glacial forest in the central part of the continent, and *Pinus* was absent. There is some controversy about the presence of *Quercus*. *Quercus* pollen is present (15%) at an Illinois site at stratigraphic levels that appear to be full-glacial (Grüger, 1972). Some authors have speculated that oak grew together with spruce under a climatic regime in which seasonality was much reduced (Wright, 1982; Solomon, 1982), while others suggest that the pollen assemblage represents a tundra in which oak pollen carried by wind from a distance stands out in a pollen assemblage from unproductive tundra (King & Lindsay, 1980; Maxwell & Davis, 1972). Oak grows together with spruce today on sandy soils in southern Manitoba, producing similar pollen assemblages (West, 1961) and macrofossils indicate that oak occurred in Iowa 12,000 years ago, when spruce was still present (Baker et al., 1980).

The deciduous forest today reaches its maximum development in the Appalachian mountains. Here the community diversity is highest and many species reach maximum size and growth rate. The high diversity of this forest community has led to speculation that the southern Appalachian region was a center for the deciduous forest community, and perhaps functioned as a refuge area during the Quaternary glaciations (Braun, 1950). The fossil record disproves this idea, *showing instead that deciduous forest was completely displaced from the Appalachian mountains.*

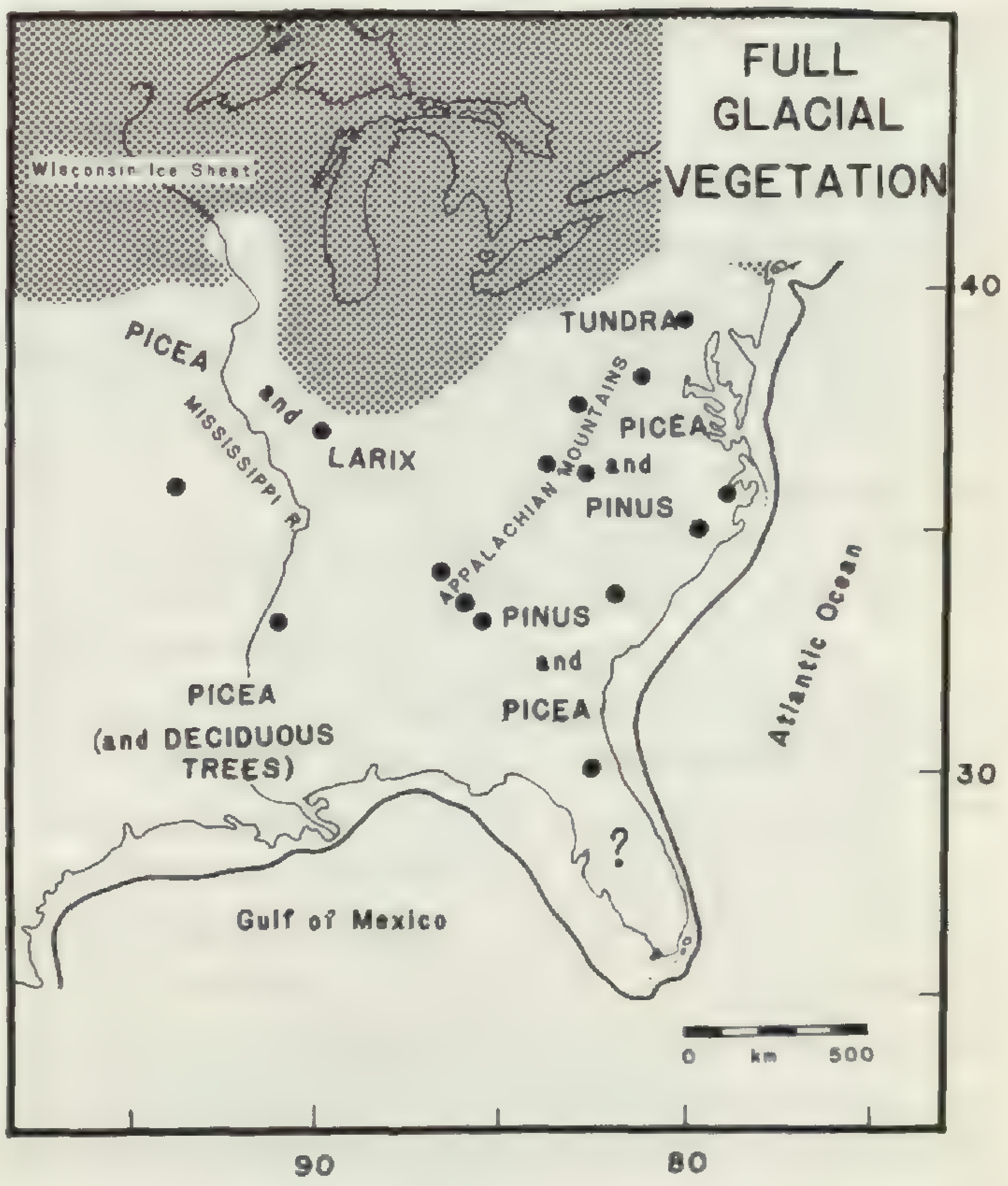

FIGURE 2. Outline map of North America, showing the extent of ice and the locations of major kinds of vegetation 18,000 years ago. Black dots indicate locations of fossil deposits dated with certainty at 18,000 to 18,500 years.

Full-glacial pollen deposits are dominated by coniferous pollen; they do not show a predominance of deciduous tree pollen, such as occurs today in modern sediment from all regions dominated by deciduous forest, especially regions of mixed mesophytic forest (Delcourt et al., 1983). Deposits dated at 18,500 years before present in northern Florida contain 80 percent pollen from southern pine species. Farther south there are no records, although sand dunes and other geomorphic evidence suggest that the region was too dry for extensive deciduous forest (Watts, 1983). It is unclear where all the deciduous forest species survived the last glacial maximum. Fossil pollen, seeds and fruits from temperate deciduous trees suggest that some species grew together with spruce near Memphis in the Mississippi Valley (Delcourt et al., 1980). In northern Florida, deciduous tree pollen (mainly *Quercus* and *Carya*) makes up 15 to 20 percent of the pollen assemblage (Watts & Stuiver, 1980). Deciduous tree pollen increases in abundance rapidly at many southern sites during the late-glacial period, sug-

gesting that at least small populations of temperate trees such as *Fagus* grew nearby in very small, scattered refuges at the time of the glacial maximum (Watts, 1984; Solomon et al., 1981).

During the coldest part of the last glacial period, small populations of deciduous tree species may have grown in unusual habitats where local conditions compensated for the regionally cold, dry climate. These refuges were small in area and scattered throughout the region, apparently comprising only a small fraction of the total landscape area. In a regional sense pine was more abundant than deciduous trees: it dominated the pollen assemblages. There was no large area 18,000 years ago that could have been mapped as a region of predominantly deciduous forest. In their recent, detailed reconstructions of full-glacial vegetation, Delcourt and Delcourt (1981) mapped the coastal plain as "Oak-hickory southern pine" evergreen forest. The existence of this forest type is not well documented, however, as evidence has not been published from sites on the coastal plain except northern Florida, where it is certain that sedimentation occurred continuously during the full-glacial (Watts, 1984). Although Delcourt and Delcourt implied a higher frequency for angiospermous trees than I have suggested, they were in agreement that the full-glacial vegetation of this region was different from the modern mixed mesophytic forest of the Appalachians.

Holocene Forests

Additional information about the history of deciduous tree species comes from records of vegetation after the ice began to retreat. In this case we have many sites, not only those in Figure 2, but also many north of the glacial boundary, where lakes and bogs are plentiful. These localities are indicated by the small numbers in subsequent figures; references are given in Davis (1981).

Pollen records were used to determine the northward movement of trees recolonizing deglaciated territory during the early Holocene (Davis, 1976, 1981). Of course pollen can be dispersed far from living populations of plants; some quantitative criterion must be developed to use pollen grains as evidence for the local arrival of trees. Modern pollen deposition rates in lakes show a relationship to geographical range limits. Accumulation rates for all species studied are higher within the range limit than outside of it, and higher still where the species is abundant. These relationships were different for the different species that were studied, depending apparently on the production rates and dispersal tendencies of the pollen. Generally, pollen deposition rates are at least 5-fold, and in some cases 10-fold higher within the range than outside (Davis et al., 1973). On this basis I have deduced that the earliest steep rise in the rate of pollen deposition in fossil deposits, that is a ten-fold increase to levels similar to those observed in modern sediments within the range of the source species, can be used as evidence of local arrival. In a few instances where data were available only as relative counts, I used a steep rise in pollen percentages in radiocarbon-dated pollen percentage diagrams. In fitting isochrones, however, more weight was given to data points based on deposition rates.

Recognizing that pollen percentages can be as low as one percent near the geographical limit for a species, I have avoided using a particular pollen percentage value to indicate presence. Low percentage values are difficult to determine accurately because of statistical errors. Macrofossils have corroborated the interpretations in many cases (Davis et al., 1980). There are also cases where macrofossils have been found at nearby sites where population expansion occurred earliest were closest to refuge areas, and sites that show later arrivals are farther north. Maps showing northward range extensions of several major forest trees have been prepared from published pollen evidence using the criteria described above (Figs. 3, 4, 5).

Arrival times (rounded to 1,000-year intervals) were indicated on a map, and isochrones were drawn connecting points of similar age. The sites where poulation expansion occurred earliest were closest to refuge areas, and sites that show later arrivals are farther north. Maps showing northward range extensions of several major forest trees have been prepared from published pollen evidence using the criteria described above (Figs. 3, 4, 5).

Figure 3, for example, shows data for *Picea*. The stippled area is the region where *Picea* grows today. The small numbers on the map show "arrival times" in thousands of years before present at each site. Isochrones have been drawn connecting points of similar age, tracing the leading edge of the expanding population. The scatter of points indicates the uncertainty of the determinations of arrival dates. Pollen percentages com-

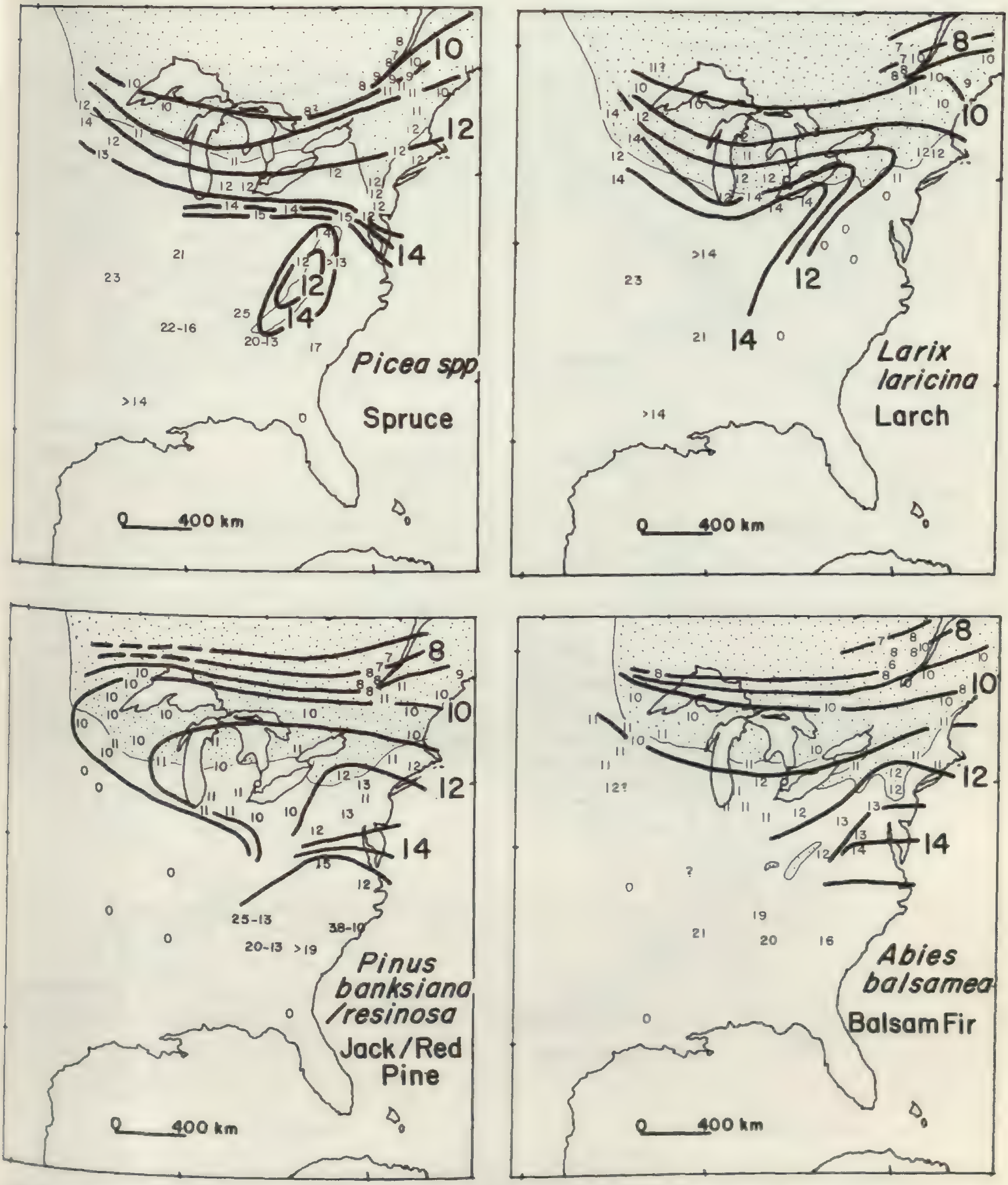

FIGURE 3. Expansion of boreal tree species northward following the retreat of the ice. Small numbers indicate arrival times in thousands of years before present at individual sites, as indicated by fossil pollen (see text). Lines connect points of similar age, indicating the location of the expanding frontier for the species at 1,000-year intervals. Shaded area is present-day range for the genus or species (from Davis, 1983).

piled from sites over a wide area have been plotted on a similar series of maps by Bernabo and Webb (1977), Webb (1981), and Huntley and Birks (1983). Pollen percentages are affected by the background of pollen produced by other species, as well as by the amount of pollen produced by the population of interest. Nevertheless a map of percentages shows the region where the species was most abundant (given a more or less constant pollen background) and it shows the

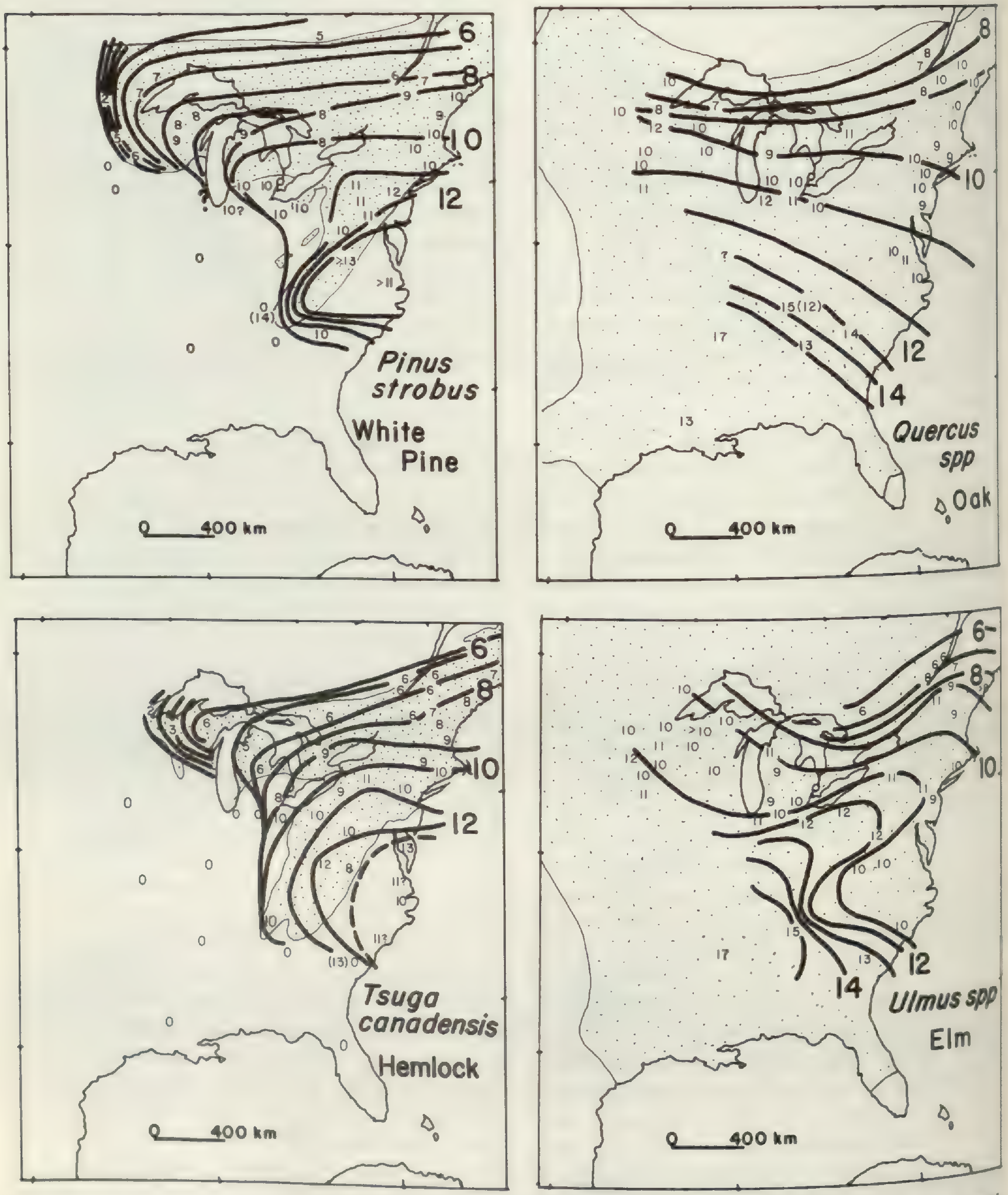

FIGURE 4. Range extension of two coniferous tree species that commonly grow in deciduous forests, and *Quercus* and *Ulmus*. Both coniferous species expanded from the eastern coastal plain, suggesting a refuge area somewhere in the vicinity. Oak and elm expanded in a northeasterly direction from refuges that were apparently located in the southern Mississippi valley region (from Davis, 1983).

retreating edge of the migrating population (Bernabo & Webb, 1977). Data showing later arrivals at northern sites than at southern sites can be used to calculate rates of range extension in meters per year. Most tree species were able to extend their ranges northward 200 to 300 meters per year, a rapid rate for trees with long generation times. These estimates are supported by data from Europe, which suggest similar rates of expansion there (Firbas, 1949; Huntley & Birks, 1983).

In northeastern United States, far from the

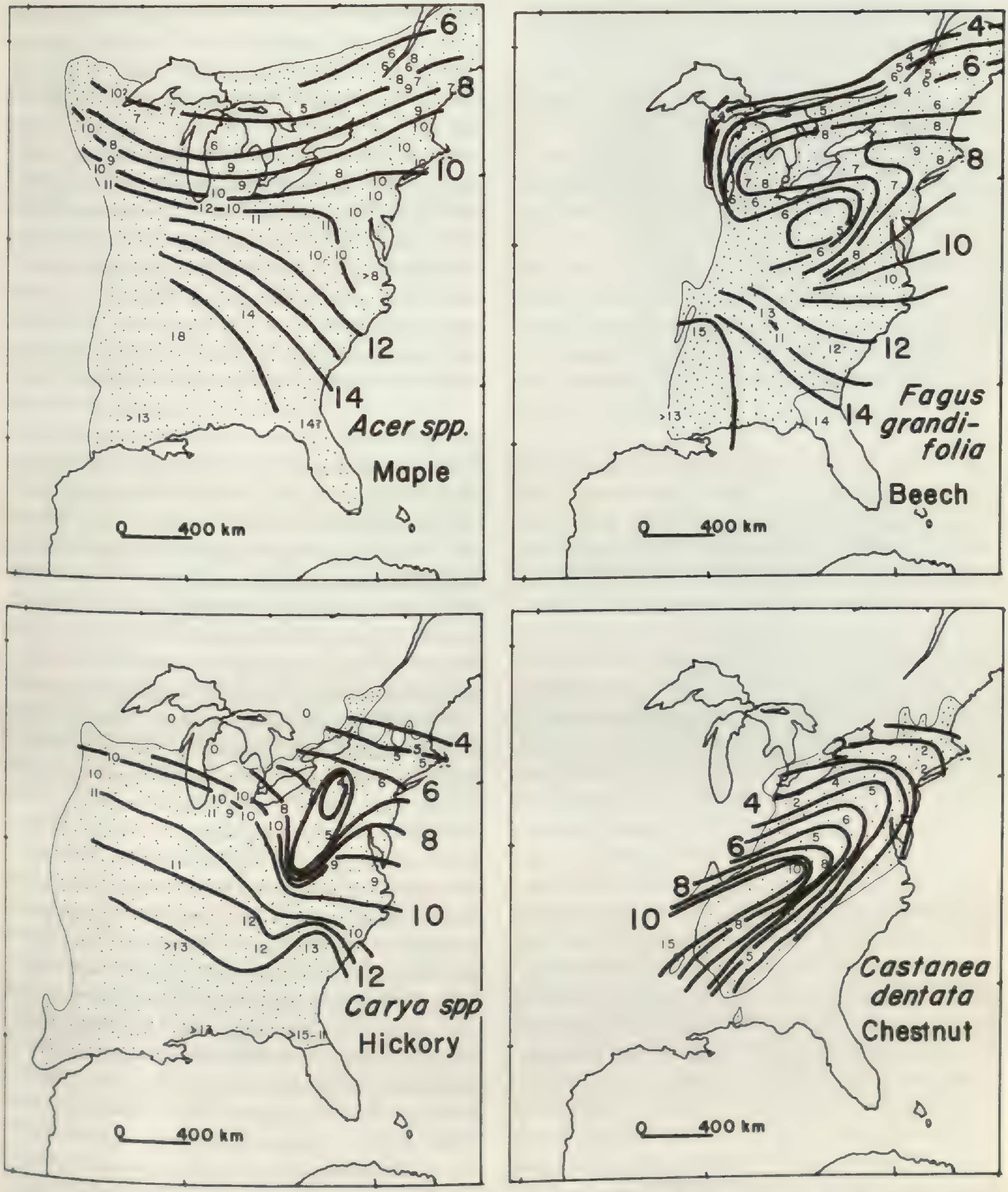

FIGURE 5. Range extension of four deciduous tree species or genera following the retreat of the ice. Chestnut was the slowest species to extend its range northward. Beech moved northward east of the Appalachians, expanding westward across the lower Great Lakes region (from Davis, 1983).

refuge areas where trees grew during the glacial maximum, the forest vegetation gained species gradually through time, increasing in diversity throughout the Holocene. Certain forest species arrived very late—*Castanea* arrived in Connecticut as recently as 2,000 years ago. Sites in the southern Appalachians, such as Anderson Pond in Tennessee (Delcourt, 1979), were closer to refuges and much less influenced by migration histories (Solomon et al., 1981).

The replacement of *Picea* and other boreal species by deciduous forest or by mixed deciduous forest was time-transgressive, occurring 16,000 years ago in the south and 10,000 years

ago farther north. The maps (Fig. 3) show that northward expansions of boreal species occurred at different rates. *Picea* and *Abies*, which have overlapping geographical ranges at the present time, did not expand northward together. In some regions, such as northern New Hampshire, *Abies* arrived after *Picea* had declined in abundance. These results refute the idea that two trees that co-occur today in a recognizable plant community necessarily expanded together in the past in response to climatic change. The rate at which each species could expand into available habitat depended not only on suitability of climate, but also on the dispersal of seeds and the ease with which new individuals could become established.

Many deciduous tree species moved into northern United States from the west as interglacial conditions developed. This group includes *Ulmus, Acer, Quercus, Carya* and *Castanea* (Figs. 4, 5). *Ulmus* (Fig. 4) ranges far north into Canada at the present time (stippled area on Fig. 4); its physiology appears adapted to the cooler climates that may have prevailed 10,000 to 11,000 years ago. *Acer* (mainly *A. saccharum*) also arrived very early at some midwestern sites, 12,000 to 11,000 years ago, expanding rapidly into the northeast, where it arrived about 9,000 years ago. The rapid and early expansion of *Quercus* is surprising, as its distribution today is temperate rather than boreal. Furthermore, it has heavy seeds that depended on animals for dispersal. Birds can be very effective dispersal agents, however, because birds such as blue jays and crows not only feed on acorns but fly considerable distances with them, caching them in wooded areas (Van der Pijl, 1969). It can be argued that animal dispersal is more effective than wind dispersal, since the seeds are carried to suitable sites rather than distributed at random. Ease of establishment may also have affected the success of *Quercus*. Its range extension was rapid, more rapid than any of the deciduous trees that today grow in mature forests. Also moving from the west, but expanding more slowly, was *Carya* spp., which arrived early (10,000 B.P.) in the Midwest, even at sites close to its present northern boundary. But it was slow to cross the Appalachian mountains and arrived late in New England, only 5,000 years before present.

Castanea pollen is found in quantity near Memphis, Tennessee, as early as 15,000 years ago (Delcourt et al., 1980). It then expanded northeastward up the Appalachian mountain chain (Delcourt, 1979). The expansion was relatively slow, averaging about 100 meters per year. *Castanea* is dispersed by birds; however, it is completely self-sterile, which may mean that the statistical chances for the establishment of populations are much lower than for self-fertile species. It was successful once it became established, becoming abundant throughout the Appalachians, and dominant in many areas (Braun, 1950). The direction of expansion of all the above-named species suggests that they survived the last glacial period somewhere west of the Appalachians, perhaps in the southern Mississippi Valley (Delcourt & Delcourt, 1981).

Fagus grandifolia (Fig. 5) moved northward along the Atlantic coast east of the Appalachians. Beech then expanded westward through the Mohawk Valley into the Great Lakes region, spreading southward into Ohio. The movement of beech into Wisconsin and Michigan is being studied in my laboratory by means of closely spaced sites; our results suggest that beech has been dispersed several times across geographical barriers 30 to 100 km wide. Detailed studies of migration histories indicate the mechanisms of dispersal for plants, and give us some idea of the role of geographical barriers in preventing or slowing geographical spread (Woods & Davis, 1982; Webb, 1982) (Fig. 5).

Two coniferous species, *Pinus strobus* and *Tsuga canadensis*, expanded from a refuge on the central coastal plain, or on the exposed continental shelf, which has long been suggested as a refuge area (Fernald, 1925). At least their pollen appeared first at sites in the mid-Atlantic region (Fig. 4). Both species then expanded westward and northward. Although *Pinus strobus* and *Tsuga canadensis* grow today in mixed stands with temperate deciduous forest species, they were not growing together with many of the deciduous trees during the last glacial period. In other words, the communities in the refuge areas were different from modern communities, composed of small subsets of the species characteristic of the diverse "mesophytic forest." This is an important point, because trees were exposed to competition from species co-occurring in refuge areas for about 50,000 years. The makeup of the communities is important when the evolutionary history of species and coadaptations between species are considered. In contrast, deciduous tree species have been growing in the Appalachians where we study them today for fewer than 12,000 years, and for less than half that time in the northern

Appalachians. In the northeast, deciduous forest communities have gained new species throughout the Holocene, increasing in diversity as additional species extended their ranges to this region.

Many communities that appear similar today have had different histories even during the last few thousand years. For example, *Quercus-Castanea* forests in the Appalachian mountains have contained *Castanea* for different lengths of time, 8,000 years in the southern Appalachians and only 2,000 years in the north. Thus, present similarities in community composition do not necessarily mean that forests have had a long, similar history.

Range limits change constantly in response to climate. For example, *Pinus strobus* moved north of its present limit about 5,000 years ago (Terasmae & Anderson, 1970), when the climate was warmer. As the climate cooled in the last few millennia, the tree has retreated southward; at the same time the climate has been getting wetter near the western limit of *P. strobus,* allowing it to expand in Minnesota (Jacobson, 1979). Species ranges are dynamic, expanding and contracting in a sensitive way in response to minor changes in climate. We have recently demonstrated that *Fagus* has also extended its range westward about 50 km within the last 1,000 years, presumably in response to recent climatic changes correlative with the "Little Ice Age" (Woods & Davis, 1982). Many range maps have been displayed and discussed at this Symposium; it should be kept in mind that many of them may represent geographical distributions that have been attained only recently, and that will change again as the climate changes.

The Holocene is similar in length and comparable in climate to previous interglacials. We must conclude, therefore, that rapid northward expansions of deciduous trees occurred many times previously during the Quaternary.

Deciduous Forests of Europe

A detailed knowledge of Pleistocene biotic history is available from Europe, where interglacial deposits have been studied in detail, making it possible to observe the timing of changes in the floristic composition of temperate forest communities. Recent work has indicated that extremely severe climatic conditions prevailed in Europe during the glaciations. Reconstructed ocean surface temperatures 18,000 years ago show

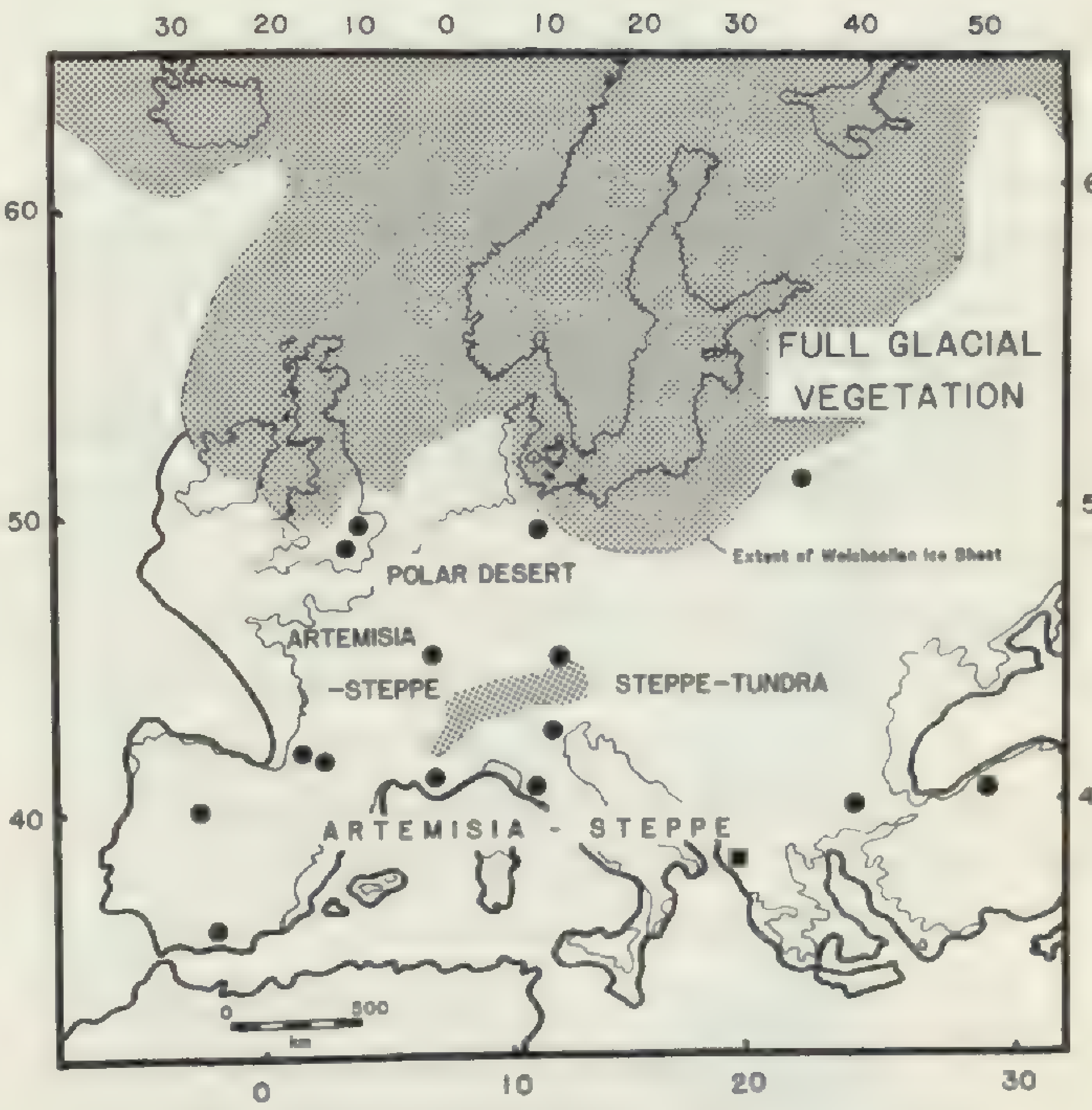

FIGURE 6. Outline map of Europe, showing the distribution of ice sheets and major vegetation types during the full-glacial, 18,000 to 20,000 years ago.

that sea ice covered the ocean as far south as Iceland and polar water flowed south to the Bay of Biscay. Surface water temperature fell 10°C. The warm Gulf Stream, instead of flowing northeastward across the Atlantic and along the western coast of Europe, as it does today, flowed eastward across the mid-Atlantic and southward past the Iberian peninsula (Climap, 1976).

Europe was without forest beween the northern ice sheet and the Alps (Van der Hammen et al., 1971). The floor of the North Sea was exposed by lowered sea levels, providing a large land area in Northern Europe and a relatively continental climate. The low countries and Denmark were "polar desert." Farther south, the vegetation was a tundra with abundant *Artemisia* (Peterson et al., 1979). *Artemisia* steppe also characterized the Mediterranean region. Similar vegetation grew in Turkey, and east to the Iranian Plateau (Van der Hammen et al., 1971) (Fig. 6). Cold and dry climate is indicated.

Pollen diagrams from interglacial deposits in Europe are similar to Holocene pollen diagrams; they show the successive arrivals of different species as trees extended their ranges northward from glacial refuges. At sites in central and northern Europe, interglacial pollen diagrams begin with a boreal flora of *Pinus* and *Betula,* and end with *Pinus, Betula,* and *Picea*; in the intervening temperate zone the diversity of the flora gradually increases as more and more deciduous tree

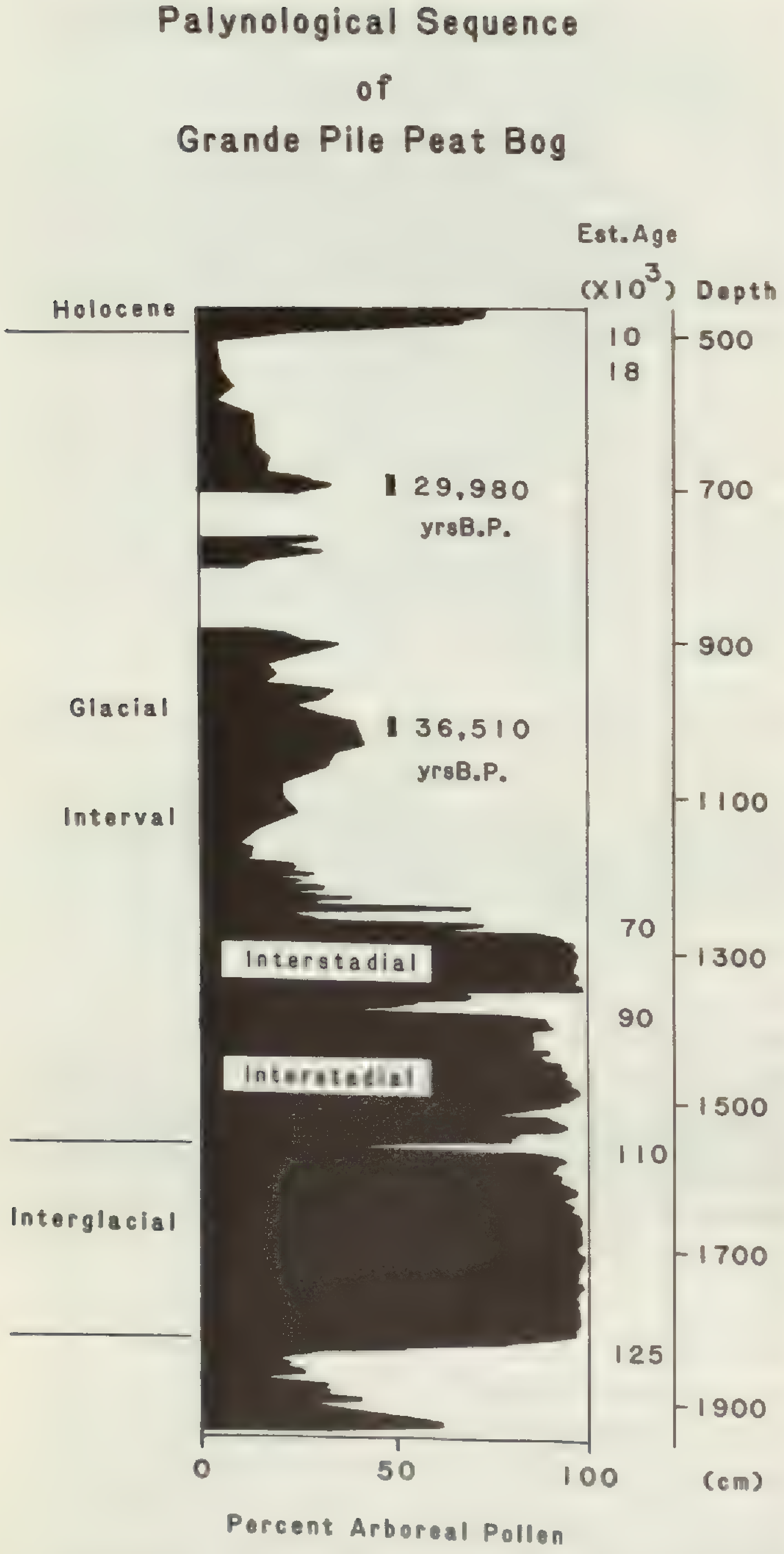

FIGURE 7. Percentages of tree pollen in the Grand Pile pollen diagram (from Woillard, 1978).

species appear. The younger interglacials and the Holocene are marked by the very late arrival of both *Carpinus* and *Picea*; these genera appeared earlier in the older interglacials.

The Grand Pile Peat Bog in northern France is a recently investigated site that is remarkable because it provides a continuous record of vegetation during interglacial and glacial intervals. A continuous sedimentary sequence includes the Holocene, the time of the last glaciation, the last interglacial and the previous glacial maximum, which occurred about 130,000 years ago (Woillard, 1978). Figure 7 is a much simplified pollen diagram that shows the percentage of tree pollen within the pollen total. The penultimate glacial maximum 130,000 years ago is marked by low percentages of tree pollen. Tree pollen was abundant during the last interglacial, which extended from 125,000 to 110,000 years ago. The interglacial terminated with a change in climate 110,000 years ago that is also recorded in deep sea sediments. Forest disappeared from the vicinity of Grand Pile and was replaced by an *Artemisia* steppe. One hundred thousand years ago, the climate became warmer again, and the forest returned. A forest succession similar to the Holocene is indicated by the pollen diagram, as all the forest species, including *Picea*, returned. *Picea* had had a late arrival during the preceding interglacial interval, but it must have been growing nearby during the subsequent cold stadial, because it was available for rapid recolonization when the climate warmed 100,000 years ago. A second cold period began about 90,000 years ago. Again, the forest was replaced by *Artemisia* steppe, and again, about 10,000 years later, the forest returned, including all tree species. Then the climate became cold again 70,000 years ago, and a long cold period ensued, culminating in the glacial maximum 18,000 years ago. During this long period, *Artemisia* steppe prevailed locally and the deciduous forest and *Picea* apparently retracted to distant refuges.

In her classic paper, Reid (1935) emphasized the importance of east-west trending mountains in the extinction of deciduous forest species in Europe. She believed that the glaciers were accompanied by cold climate, which caused extinctions of temperate trees everywhere north of this mountain barrier. Only those species that reached refuges in the Mediterranean survived. Reid's discussion emphasized the onset of glaciation as a time of extinction. The Grand Pile data imply, however, that although forest disappeared locally in response to cold climate at the onset of glaciation, all species were available to return as soon as the climate became warm again. A more important extinction time was the very long and very severe cold period that included the glacial maximum (70,000 to 16,000 years ago), rather than the first onset of cold 100,000 years ago that accompanied the development of continental ice sheets. It was during long cold periods, lasting 50,000 years or more, that trees like *Picea* became locally extinct, surviving only in refuge areas far to the east. When the next interglacial, the Holocene, began, *Picea* was slow to return to western Europe—in fact it never did return during the Holocene to the vicinity of Grand Pile.

Distributions of deciduous trees expanded in

Europe during the Holocene just as they did in North America. It seems likely that somewhere on the southern slopes of the Alps and/or in the Balkans there were habitats during the full-glacial that were suitable for deciduous trees (Van der Hammen et al., 1971); probably small populations were scattered about in pockets of favorable environment. Maps of Holocene pollen frequencies in Europe show that many deciduous tree species expanded first in southeastern Europe and then moved westward (Huntley & Birks, 1983). The gradient in ocean surface temperature across the Mediterranean (Climap, 1976) may have been correlated with more favorable temperatures on land as well.

The succession of interglacial deposits in Europe record the progressive extinctions of tree species during the Quaternary (West, 1970; Wolfe, 1979). Different interglacials witnessed the development of different communities of deciduous trees, depending on which species arrived in the British Isles. Floristic differences among the British interglacials were also caused by evolutionary changes. West (1980) suggested that *Picea,* for example, which appeared in Britain during early interglacials, must have been migrating to the British Isles from refuge areas in western Europe. In the later interglacials there was a gradual loss of biotypes that were able to survive in refuges in western Europe. *Picea* appeared later and later in successive interglacials, and during the Holocene it failed entirely to expand into Great Britain.

Additional evidence for evolutionary changes is provided by *Corylus* pollen percentages in the successive British interglacials (West, 1980). In the early interglacials of East Anglia, *Corylus* pollen percentages are low. Later in the Quaternary it became more abundant, and finally, in the Holocene, it arrived early and built up a large population before other deciduous trees arrived. West suggested that *Corylus* may have adapted to interglacial conditions. Whereas *Picea* was less and less successful, and *Tsuga* became extinct altogether, *Corylus,* a deciduous angiosperm, became more and more abundant.

Discussion

Extinction rates in Europe during the Quaternary were higher for coniferous trees than for temperate deciduous angiosperms (Wolfe, 1979). The preferential elimination of conifers documented in Quaternary deposits led to the development of the predominantly deciduous forest that we see today in northwestern Europe. Two factors may have selected against conifers during the Quaternary: 1) they might not have been able to expand into forested landscape as successfully as the deciduous trees, thus losing out in competition during the interglacials. The successful invasion of beech forests by spruce during the last few centuries (Moe, 1970) argues against this. There is some evidence, however, that the migration of *Picea* is influenced by soil changes, especially progressive leaching of calcareous soils (Andersen, 1964). If so, the expansion of *Picea* could have been delayed by unsuitable soils in the early part of the interglacial. This theory does not explain *Picea*'s history during the early Quaternary, however, when it appeared during the early phases of interglacial sequences in Britain.

2) Alternatively, conditions in the refuge areas might have selected against conifers. The extinction of western European populations of *Picea* mid-way through the Quaternary (West, 1980) may be related to the very severe conditions that existed during the glacials in the western Mediterranean region. A very dry and probably continental *glacial* climate may have selected against spruce, even though *interglacial* climates, like the Holocene, were favorable for conifers. It would be a mistake to study the present climate and try to use it to explain all aspects of the distribution of the modern flora (Wolfe, 1979). Instead, the longer intervals of time during which the climate was very different must be taken into account, i.e., the glacial intervals, which comprise nine-tenths of the Quaternary Period. During these longer intervals, extinctions of conifers occurred, although many temperate angiosperms were able to survive.

The Quaternary fossil record has further implications for the geoflora concept. Geofloras are forest communities that were believed to persist, unchanged in composition, over many millions of years. In contrast, Holocene forest communities are ephemeral, composed of newly immigrated species, and easily invaded by additional species. The deciduous trees growing in our forests that have persisted from Tertiary time are aggressive species that have been able to move rapidly onto deglaciated territory. Any species that has not been able to disperse its seeds easily, to extend its range, and to penetrate forest communities, has become very rare or extinct. Wolfe (1979) compares our tree flora to secondary species in the forests of eastern Asia. The nature of modern communities calls into question whether the concept of closely co-adapted com-

munities such as "geofloras" is appropriate to describe Tertiary forests.

The deciduous forest communities of eastern North America and western Europe remain a grab-bag of species with characteristics that enabled them to survive during the Quaternary in the very unstable environment of interglacials, when rapid dispersal and colonization abilities were selected for. During the glacials, dry and continental climate exerted a different kind of selective pressure. Campbell (1982) has compared the tree floras of Europe and eastern North America, invoking these factors to explain some of the differences. The modern deciduous forests are a product of Quaternary history over the last two million years. Although on the generic level the forests of eastern North America bear a similarity to Tertiary forests of the same region, the marked changes that have occurred in Europe caution us against using the present forest as a model for the forests of the Tertiary.

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THE TIBETAN PLATEAU IN RELATION TO THE VEGETATION OF CHINA

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Vegetation zones of the eastern coast of China represent a series of forests from the tropical to the cold-temperate zone. There is also a change from forest through steppe to desert from the southeastern coast to the northwestern interior (11). These patterns are quite different from those in western Eurasia where the vegetation pattern of the western part from south to north is: tropical, subtropical desert and savanna, Mediterranean sclerophyllous forest, deciduous forest, and coniferous forest. This series shows a pattern, drier in the south and moister in the north, that basically reflects Hadley's classic diagram of atmospheric circulations (10, 25, 26, 28). Therefore, the differences between the eastern and western parts of Eurasia reflect an "asymmetric" distribution of vegetation (Fig. 1). The geographic distribution of vegetation in China-Eastern Asia should be interpreted primarily in terms of patterns of atmospheric circulation in Asia because it reflects the "projection" of atmospheric circulation onto the land surface of the earth.

Recent research in atmospheric physics indicates that the Tibetan Plateau in eastern Asia is a huge "Hot Island" that hinders atmospheric circulation (5). The powerful thermal and orographic effects of the Plateau cause great changes in the atmospheric circulation of the northern hemisphere, especially in Asia, and have a direct effect on patterns of vegetation in that part of the world.

Hereafter I will discuss the uplift of the Plateau in relation to atmospheric circulation and the distribution of vegetation in China. The most important events in this regard are the formation of the Tibetan High, the establishment of the Mongolian anticyclone, and the reinforcement of the Eastern Asian Monsoon.

Formation of the Tibetan High and the Plateau Zonation of Vegetation in Tibet

The Tibetan High, which arises from the powerful thermal effect of the Plateau in the summer and the cooling effect of the Plateau in the winter, is a vast system of the atmospheric circulation in the upper atmosphere (5) (Figs. 2 and 3). Its center is located in Ali, the western part of the Plateau. This region has very little precipitation—only about 50 mm annually—and is therefore a desert or semidesert climate. Figure 4 shows the extent of the resulting vegetational region. The vegetation is suffrutescent desert and steppe-desert types that are composed mainly of *Ceratoides latens*. In the northwestern part of the Plateau, the climate is very dry and cold by reason of high altitude and its more northern latitude. A sparse high-cold desert of low suffrutescent and cushionlike *Ceratoides compacta* has developed there. On the vast flat of the central Plateau, the annual precipitation increases to about 200 mm, and a high-cold steppe vegetation of *Stipa purpurea* prevails. This is the major vegetation type of the Plateau. In the eastern part of the Plateau there is a cold, low-pressure zone where annual precipitation reaches 600 mm. Under this cold and wet climate, a special kind of high-cold meadow has developed, consisting of *Kobresia* and low scrub *Rhododendron*. Therefore, the Plateau vegetation changes from southeast to northwest, grading from high-cold meadow and scrub through high-cold steppe and desert to high-cold desert. This sere of high-cold vegetation was formed and developed in the Quaternary.

The Tibetan High influences not only the Plateau itself, but is also the center of a great high-pressure belt above Asia, North Africa, and southern Europe. Around the periphery of the Tibetan Plateau, there exist striking differences in climate and vegetation: the southern side of the Plateau is the wet, rainy, and steep slope of the Himalaya Mountains, falling to the India-Bengala plain. In Assam, in the foothills of Eastern Himalayas, the annual rainfall exceeds 10,000 mm, making this one of the rainiest areas in the world. Luxurious tropical mountain forests have developed there. On the opposite, northern side of the Plateau are the Kunlun Mountains. These

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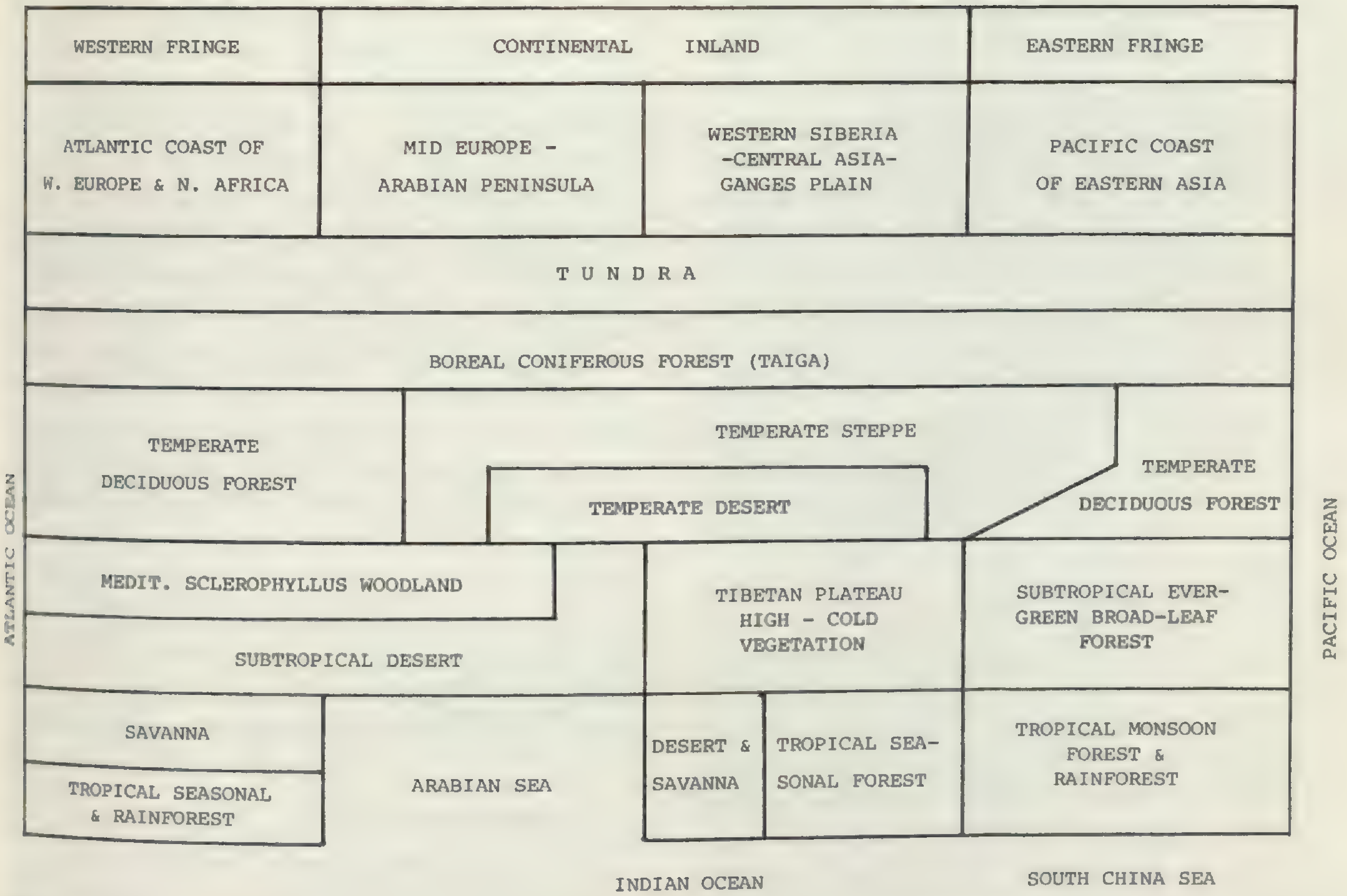

FIGURE 1. Asymmetric distribution of horizontal vegetational zones in Eurasia and North Africa.

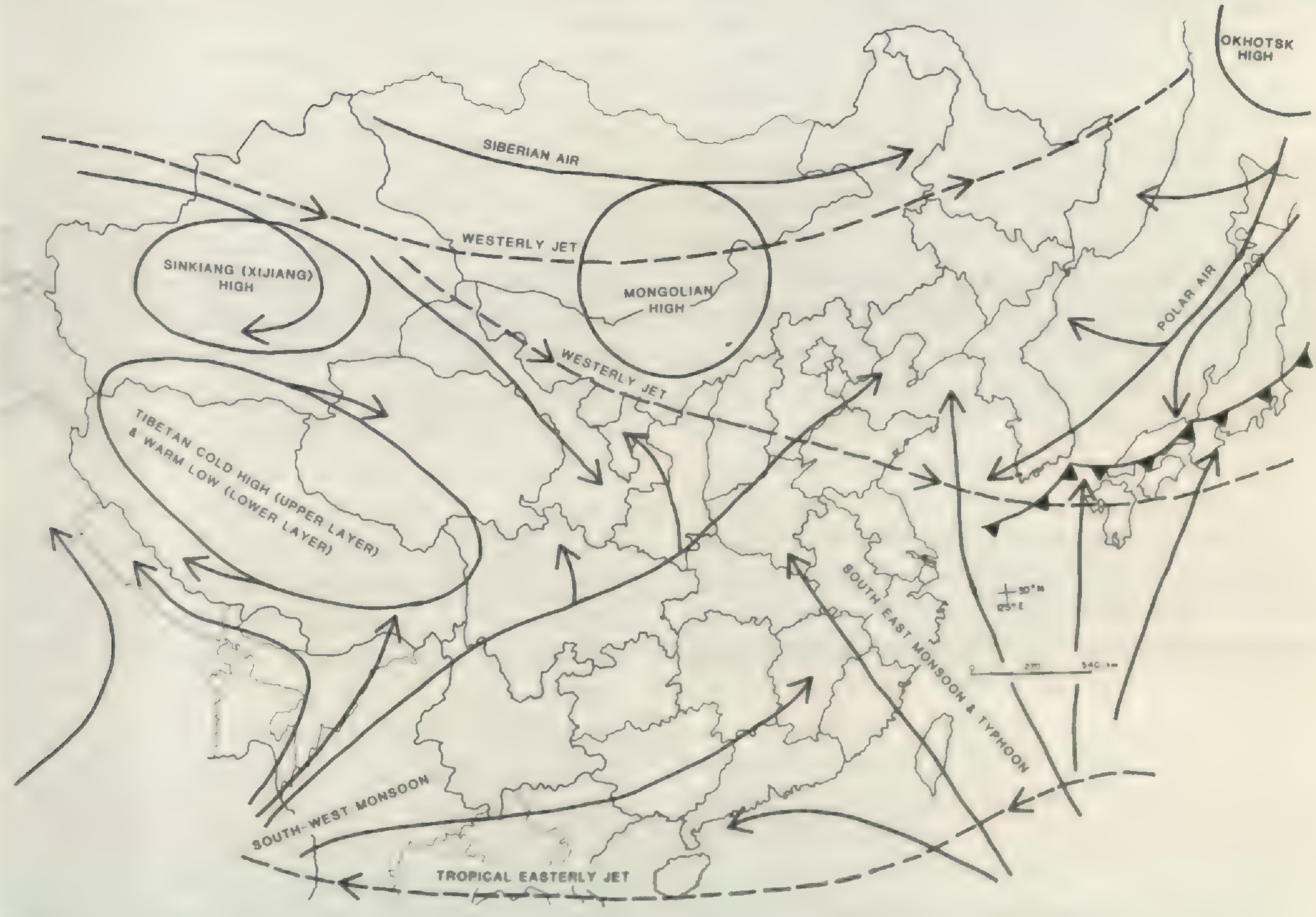

FIGURE 2. The summer circulation above East Asia (22).

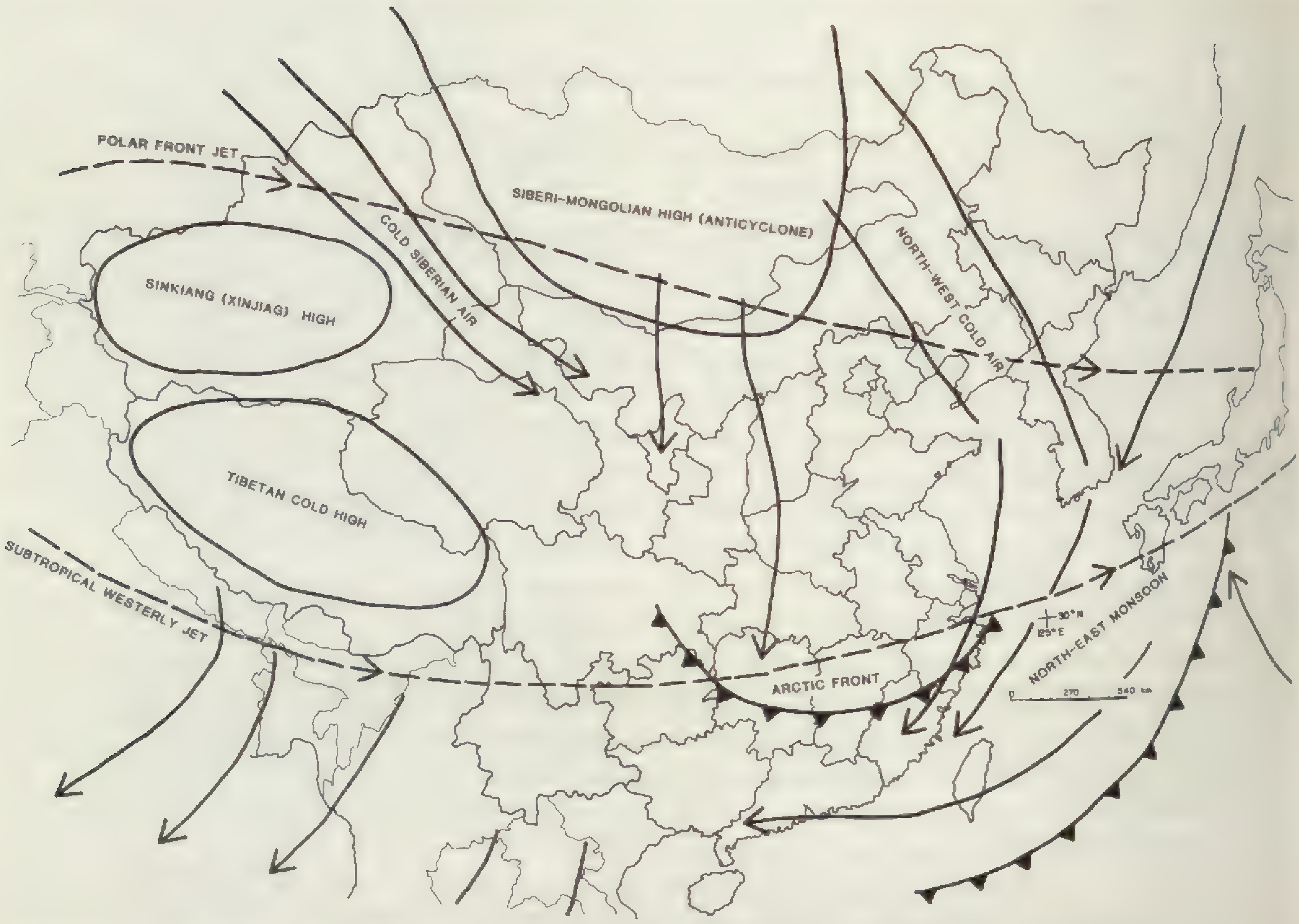

FIGURE 3. The winter circulation above East Asia (22).

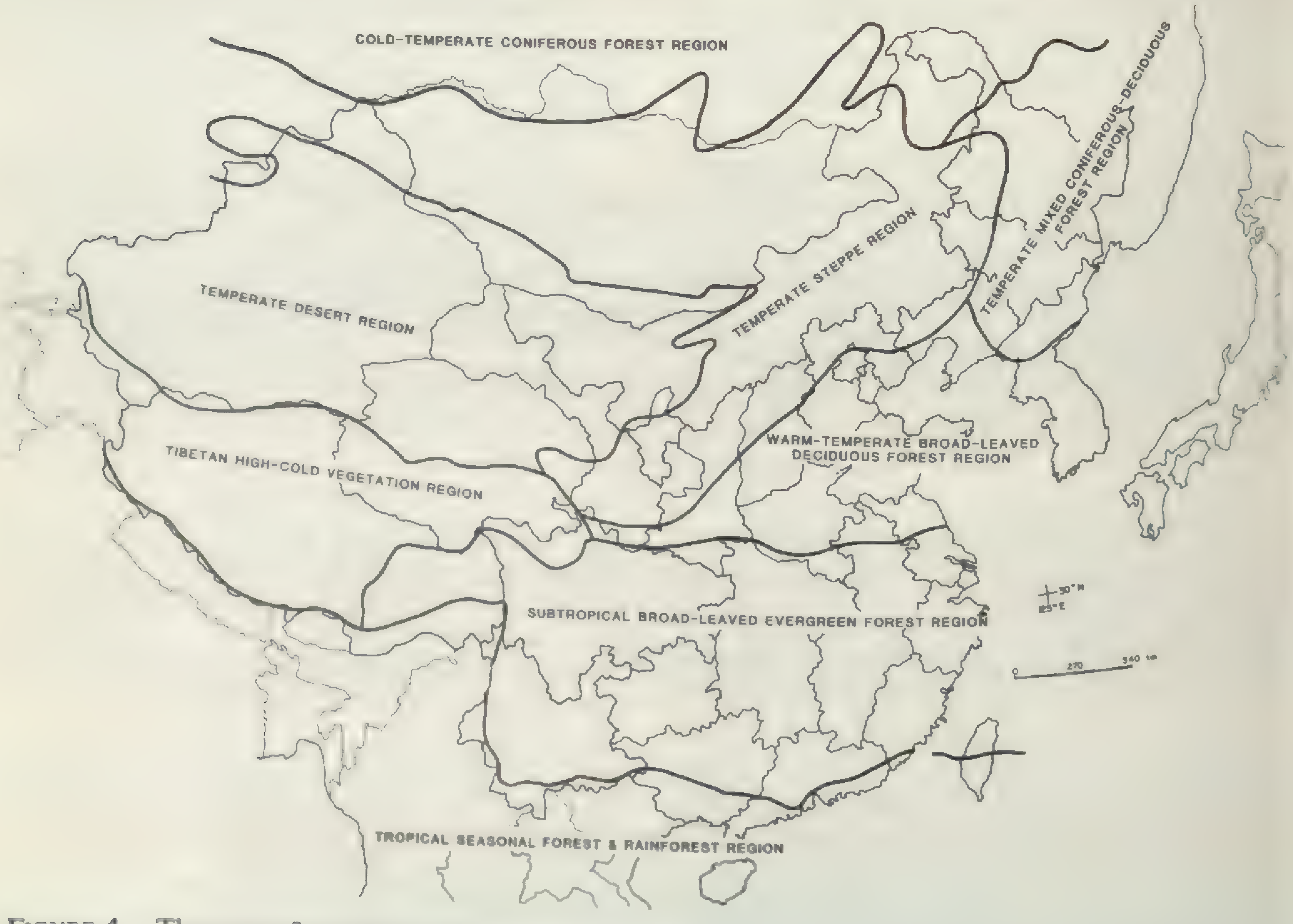

FIGURE 4. The map of vegetational regions of East Asia.

are the driest mountains in the world. Desert vegetation covers the mountain slopes from the foothills up to the snowline. At the base of the Kunlun Mountains there is a vast expanse of sand desert, the Taklamakan—the arid core of Asia, where annual precipitation is less than 10 mm. East of the Plateau, across the Traverse Mountain Range and reaching to the shore of the Pacific Ocean, is an extensive subtropical evergreen broad-leaved and temperate deciduous broad-leaved forest. To the west of the Plateau, through the arid, hot, and desert valley of Kashmir, extending to the Middle East and the west coast of North Africa, is the greatest area of subtropical desert in the world. Therefore, the Tibetan Plateau is a "crossroads" for vegetation and a climatic "watershed divide" in the Old World. The different vegetation zones on the Plateau itself reflect the close connection of the climates, floras, and vegetation types of the Plateau to the surrounding areas.

The Northward Movement of the Westerlies, Establishment of the Mongolian-Siberian Cold High, and Formation of the Desert Vegetation in Central Asia

The Westerlies are located at about 30°N latitude. They represent a system of high pressure circulation that controls the formation of arid zones. Within this zone, the climate is dry, precipitation is rare, the continentality is strong; great sand deserts are found in this zone. The Westerlies form the "desert zone of Cancer" in the tropical and subtropical latitudes. The Tibetan Plateau, which is situated between 30° and 40°N latitude, is a hugh orographic dynamic and thermal hindrance to the Westerlies. The Westerlies divide into southern and northern branches at the western end of the Plateau. In the summer, the northern branch shows an anticyclone curve in northern Sinkiang, situated on the north side of the Plateau. A high pressure zone caused by the compensational descending effect of the Tibetan High occurs above Gansu and Sinkiang. A powerful anticyclonic system—the Mongolian-Siberian Cold High—caused by the Plateau preventing thermal exchange between Siberia and the Indian Ocean, and causing an accumulation of cold air over the continent, is formed in winter. This Mongolian Cold High is the controlling system of the eastern Asian weather during the winter. It makes the winter climate cold, dry, and lacking in precipitation in this area, and has caused a vast temperate desert zone to develop in the plain of Central Asia. It ranges from Iran to Sinkiang, Gansu, Qinhai, Inner Mongolia of China, and Western Mongolia. Its northern limit reaches nearly to 50°N latitude; far beyond the limit of the "desert zone of Cancer."

According to computer simulations by Manaba, the great high pressure system was produced over continental Siberia on the north side of the Plateau only after the Plateau was uplifted. If the Plateau were eliminated, the desert areas of Central Asia would have a moist climate that would support forest or grassland vegetation and the wet, hot, and fertile plain of India would be an arid zone (4, 21). Research in Chinese geology and paleobotany has also established the following: before the Tibetan Plateau had arisen and the Tethys Sea had disappeared, there was an arid and hot climate in central China, but it was much warmer and moister in Dzungaria, which had a forest-steppe climate and vegetation at that time. After the uplift of the Plateau and the westward movement of the Tethys Sea, the climate in central China became moist, and in northern China the climate changed from warm and moist to cold and dry. The northwestern part of China became a temperate desert (7). The formation of deserts proceeded with uplift of the Plateau and moved gradually northward (4).

The Plateau prevents the effects of marine monsoons reaching the Central Asian desert region. Only a remnant of the Southwestern Monsoon reaches the Alasan and Hexi Corridor in the summertime, and then causes a concentration of precipitation. Therefore, there have developed some annual summer ombrophiles in the flora that are characteristic of the eastern Central Asian desert. Dzungaria is located in the western part of Central Asia and receives some of the Mediterranean subtropical air masses. This causes more spring rainfall and has led to development of a vegetation containing spring-ombrophiles, which are characteristic of the western Central Asian desert. The Beishan Gobi, East Sinkiang, and the eastern part of South Sinkiang are located in the most arid core of the desert, and are under the influence of the center of high pressure and powerful anticyclone. There is very little precipitation, usually not more than 10 mm. The desert vegetation is sparse, and there often appear vast bare areas of the "Gobi," drift sand, and "Yardang."

Expansion of the Steppe Vegetation and Compression of the Deciduous Broad-leaf Forest by the Effect of the Mongolian Cold High

There is no significant orographic hindrance to atmospheric circulation in the eastern part of Asia. Therefore, the cold Mongolian-Siberian anticyclone caused by the uplift of the Tibetan Plateau invades southward in Eastern Asia. This has permitted steppe vegetation, which is adapted to arid and cold continental climate, to expand southeastward. This has restricted the area of the mesic deciduous broad-leaf forest, which requires a temperate, moist climate. Several thousand years of agricultural activity have destroyed the primeval forest vegetation in the central plains of China (the Yellow River Basin), one of the original centers of ancient culture, and accelerated the development of the steppe. Generally, the area of broad-leaved deciduous forest in eastern Asia is more limited and smaller than that in Western Europe and North America. It disappears abruptly in the central part of eastern Asia. The spring drought and the cold winter that are caused by the Mongolian High are the most important limiting conditions for development of broad-leaved deciduous forest in eastern Asia.

The temperate steppe zone, which crosses the center of Eurasia, bends southward in eastern Asia and reaches it southern limit at 34°N latitude, a large southward deviation. The eastern Asian steppe zone is transitional between the arid-cold climate controlled by the Mongolian-Siberian High and the moist climate under the influence of the eastern Asian Monsoon Low. The steppe zone can be divided into three transitional subzones: the desert-steppe, the typical steppe, and the forest-steppe. Communities in these subzones are dominated by various steppe grasses. The subzones conspicuously reflect the transition from arid to semi-moist climate, and from desert to forest vegetation.

Aleutian Low and Presence of the Northeastern Mixed Needle-Broad-leaf Forest

A temperate, mixed, needle-broad-leaved forest type is distributed in the northeastern part of eastern Asia (Northeast China, North Korea, and the Soviet Far East). Its dominant, Korean pine (*Pinus koriensis*), requires a moist maritime climate. The persistence of this mesic forest type might be under the influence of the Taiwanese warm current—the Black Tidal Current, which passes by the coast of northeastern Asia, creating a moist and rainy climate (27). In terms of atmospheric circulation, eastern Asia is mainly under the control of the Aleutian Low in the winter, and transitional between the hot Tibetan Plateau and the cold Okhotsk Sea in the summer. The northern limit of the effect of the warm-humid Eastern Monsoon, which produces abundant precipitation, is in this region. Therefore, eastern China is more moist than northern China, and serious droughts are rare.

According to the research of Kasahara and Asakura (21), if the Tibetan Plateau were not present, the Aleutian Low and the Okhotsk High might not form or might be unstable. It might be, then, that the Plateau affects the distribution of the northeastern mixed needle-broad-leaved forest.

Not more than 500 km from the coast, the maritime climate is replaced by a continental climate controlled by the Mongolian High, and the mesic mixed forest disappears. Beyond the taiga of the Great Xingan Mountains, the vegetation rapidly becomes steppe.

Prevalence of the Eastern Monsoons and Development of the Broad-leaved Evergreen Forest

The subtropical climate of southern and southeastern Asia is controlled chiefly by the hot low-pressure system of the Southeastern and Southwestern Monsoons in the summer. In the winter it is influenced strongly by the Mongolian Cold High. In this region monsoons are more strongly developed than elsewhere and are mostly a result of the presence of the Tibetan Plateau. The effects of the Plateau are:

The importance of the Southwestern Monsoon (21). There is a branch of the humid Southeastern Monsoon that comes from the Indian Ocean, passes over the mountains of western Yunnan and Burma, and blows into continental Eastern Asia in summer. It converges with the northwestern current at 30–36°N latitude, and produces abundant summer rainfall and the "Plum rains" in the Yangtze-Huai River Basin. This precipitation is an important water supply for the southern and southeastern Asian subtropical broad-leaved evergreen forest.

The stabilization and reinforcement of the Southeastern Monsoon. The restriction on the Westerlies and the thermal effect of the Plateau increases and maintains the stability and intensity of the monsoons in Eastern Asia. This permits the monsoons to reach to both northerly

and southerly extremes (15, 16). The reinforced summer monsoons bring abundant rainfall, which is a major factor for the development of the southern and southeastern Asian broad-leaved evergreen forest.

The tropical cyclone. Typhoons also have an important effect of increasing the water supply for the eastern Asian broad-leaved evergreen forest. The Tibetan High is a strong influence in turning typhoons northward.

The southwestern low vortex. This powerful vortex forms on the plateau and moves eastward in the summer. It is an important weather system, producing summer rainstorms in eastern Asia.

Therefore, the Tibetan Plateau is an orographic and thermal factor that maintains, reinforces, and even forms the eastern Asian Monsoons and other weather systems. Its effects are indispensable for the development of the southern and southeastern Asian subtropical broad-leaved evergreen forest. The savanna or thorn scrubs of subtropical desert do not develop in a monsoon climate. Only a few relicts of these types of vegetation are present in rain shadows of the dry and hot valleys of the Traverse Mountain Range, where there is a hot low-pressure system formed by the descent and convergence of the Westerlies.

Establishment of the Tropical Easterlies and Distribution of the Tropical Rainforest and Monsoon Forest in Southeastern Asia

The powerful Easterlies, which occur south of 20°N latitude in southeastern Asia, India, and North Africa in the summer, are one of the high-level circulation systems that control the climate of these tropical areas (19). They are supported by the Tibetan High and Saharan High (23) and are especially prevalent at the south edge of the Tibetan Plateau. Some meteorologists emphasize that the Tibetan High affects the presence of the Easterlies, suggesting even that the Plateau was the basic cause of their establishment (22, 24). The Easterlies bring abundant rainfall into southern Asia and are the major supplier of water to the tropical forests in this area. Where they cease in winter, the dry season of such tropical areas, the tropical deciduous forest enters dormancy. In North Africa and the Middle East, there is a powerful descending air-flow on the southern side of the Easterlies, causing a vast area of tropical desert.

The Southwestern Monsoon, caused by the uplift of the Plateau, has had an important effect on the development of the tropical rainforest in the southwestern part of tropical China, India, and the Peninsula of Middle South. The warm, humid air of the Monsoon comes from low altitudes over the Indian Ocean and blows into Bengala and the eastern Himalayas. It is transformed into a cyclone curve by the horseshoe-shape of the mountain barrier, and produces abundant rainfall in the mountains. The annual precipitation of 5,000 to 10,000 m maintains luxuriant montane tropical rainforests and seasonal semi-evergreen forest. Because of the orographic and humid-hot monsoon effects, the tropical montane forests reach their northernmost limit here at 29°N latitude. The tropical seasonal forests of Xishuangbanna in Yunnan are also supported mainly by the Southwestern Monsoon. However, as the cyclonic winds of the eastern Himalayas turn westward and become an east wind along the southern foothills of the Himalayas into Punjab, the rainfall decreases significantly westward and the dry season becomes more severe. Thus, there are no rainforests on the southern foothills of the central Himalaya Mountains. Instead, there are monsoon forests that are mainly composed of the deciduous *Shorea robusta.*

Additionally, the Tibetan Plateau becomes a hindrance in the western part of Eastern Asia in the invasion of the Siberian cold current in the winter. This is an important reason for the northward deviation of the limit of tropical vegetation there. Because of this obstruction, the Yunnan Plateau, the eastern Himalayas, and the Indian Peninsula are rarely invaded by cold currents. The temperature in the winter there is higher than that further east. Because the eastern plain of China lacks the protection of high mountains, the cold current from the Mongolian Cold High can reach to the far south, producing cold waves in the southeastern subtropical and tropical zones, leading to cold injury of rubber trees, bananas, and other tropical crops, and pushing the tropical limit southward to the Tropic of Cancer. Therefore, the northern limit of tropical vegetation in China reaches higher latitudes in the west than in the east.

Conclusions

Neogene-Quaternary uplift of the Tibetan Plateau greatly changed and fragmented the zonal vegetation pattern that would have otherwise prevailed in much of eastern Asia. The major expressions of these changes are: the formation of the high-cold plateau vegetation zones; the

northward extension of the subtropical desert zone and formation of temperate desert in Central Asia; the expansion of the temperate steppe zone to the east and south; the restriction of broad-leaved deciduous forests; the preservation of the mixed needle-broad-leaved forest in northeastern Asia; the reinforcement of the eastern Asian Monsoon region causing an expanded development of the south and southeast Asian subtropical broad-leaved evergreen forest, instead of subtropical savanna and desert there; and the modified northern limit of the tropical forest zone in parts of southern Asia. These features of vegetation zonation, all the result of the uplift of the Tibetan Plateau, are unique to Eastern Asia.

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A COMPARATIVE STUDY OF THE VEGETATION IN HUBEI PROVINCE, CHINA, AND IN THE CAROLINAS OF THE UNITED STATES

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The study of the floristic relationship between Eastern Asia and North America involves many complex problems that concern both time and space. Timewise, a researcher can devote his time looking for paleobotanical information as well as studying current components of the vegetation of the areas concerned. Spacewise, the study can involve extensive research of widespread genera with disjunct distributions as well as intensive investigations of paired species occurring in limited areas. My report represents the result of field observations and herbarium and library investigations of two comparable areas: Hubei Province in Central China and the Carolinas in Eastern U.S.A. It covers the geographic background and general aspects of the floras of the two regions, and compares the similarities and differences of the vegetations they support.

GEOGRAPHICAL BACKGROUND AND GENERAL ASPECTS OF THE FLORAS

Hubei, a medium-sized province in central China, has an area of 187,000 square kilometers and is located in the middle portion of the Yangtze Valley, between 29°05′ and 33°20′ north latitude. It is surrounded on three sides by mountains, with the higher ones in the northwest reaching 3,000 m or more in elevation. Eastern Hubei is hilly and the central-southern portions of the province form the Jianghan Plain.

The flora of Hubei is one of the richest in China, especially in the western Hubei mountainous region where remnants of virgin forests are preserved. According to preliminary investigation, the province has about 3,816 species and 242 varieties of vascular plants belonging to 1,165 genera and 207 families. This flora is composed of tropical, subtropical, and temperate elements.

Evergreen coniferous forests occur in some of the higher elevations of the mountains in western Hubei. Small deciduous forests occur at some intermediate elevations, but usually the deciduous and evergreen coniferous species intermingle. At lower elevations, some areas are occupied by broadleaf evergreen forest. Limestone areas are sometimes occupied by *Cupressus funebris*, especially where the rock is near the surface, as in the Changjiang (Yangtze) Gorges.

The predominant species of deciduous trees in Hubei belong to the following genera: *Fagus* (*F. longipetiolata, F. lucida, F. engleriana*), *Castanea* (*C. seguinii, C. mollissima*), *Quercus* (*Q. acutissima, Q. acutidentata, Q. aliena, Q. variabilis, Q. fabri, Q. glandulifera* var. *glandulifera, Q. glandulifera* var. *brevipetiolata*), *Betula* (*B. luminifera, B. insignis, B. utilis*—all in western Hubei mountains), *Carpinus* (*C. fargesiana, C. fargesii*), *Juglans* (*J. regia, J. cathayensis*), *Pterocarya* (*P. stenoptera, P. hupehensis*), *Platycarya* (*P. strobilacea*), *Acer* (*A. davidii, A. mono, A. amplum, A. wilsonii*—most in western Hubei mountains), *Populus* (*P. adenopoda, P. davidiana, P. wilsonii, P. lasiocarpa*—most in the western part of the province), *Sorbus* (*S. alnifolia, S. wilsoniana, S. hupehensis, S. folgneri*—most in western Hubei mountains), and *Tilia* (*T. tuan, T. oliveri*—in western Hubei mountains). The major species of the broad-leaved evergreen trees belong to these genera: *Quercus* (*Q. glauca, Q. fargesii, Q. myrsinaefolia, Q. engleriana*—most in western Hubei mountains), *Castanopsis* (*C. tibetana, C. sclerophylla*), *Lithocarpus* (*L. glaber, L. henryi*), *Phoebe* (*P. neurantha, P. chinensis*), and *Cinnamomum* (*C. camphora, C. wilsonii, C. bodinieri*—most in western Hubei mountains). The major evergreen conifers are *Pinus massoniana* and *Cunninghamia lanceolata*, which usually occur in areas below 1,200 m in elevation. *Pinus armandii* occurs between 1,200 m and 2,500 m in northwestern Hubei, and *Abies fargesii* and *Abies chensiensis* occur at the higher elevations in the northwestern portion of the province.

We visited and collected specimens in the

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southern Appalachian mountains in April to late June and September, 1982. Although our visits were short (three months), the field observations and a study of the American botanical information obtained from literature have convinced us that Hubei Province and the Carolinas, even though separated by a great ocean and thousands of miles of land, are very similar, not only in their climates, but also in the vegetation.

North Carolina and South Carolina are bordered by the Southern Appalachians on the west and by the Atlantic Ocean on the east. This area has a total area of 217,000 square kilometers, and lies between 32° and 36°40′ north latitude, a little further north than Hubei Province. The Carolinas are naturally divided into three physiographic regions: the Mountains in the west, the Piedmont, and the Coastal Plain in the east.

In general, the mountains of the Carolinas are similar to the western Hubei mountainous region. They vary in height from about 350 to 2,025 meters: Mt. Michell at ca. 2,025 m is the highest mountain in North America east of the Mississippi River. In western Hubei, the mountains are somewhat higher, with an average elevation of 1,000 meters. The highest peak, Nonname Peak, in the Shennongjia Forest District, reaches 3,105 meters.

On some of the high summits of Carolinian mountains occur fir forest of *Abies fraseri* and spruce forest of *Picea rubens*. The forests of most areas below the fir and spruce forests are composed of mixed deciduous species of *Quercus* (*Q. alba, Q. rubra, Q. coccinea*), *Betula* (*B. lutea, B. lenta, B. nigra*), *Fagus* (*F. grandiflora*), *Acer* (*A. rubrum, A. saccharum, A. spicatum, A. pensylvanicum*), and *Tilia* (*T. americana*).

There are two species of *Liriodendron*, one from China, and the other from the United States. In western Hubei, small areas of pure *Liriodendron* forest are rare; usually it is mixed with other species and is not abundant. The American species, *Liriodendron tulipifera*, is common in the Carolinas, where there are large areas of pure yellow poplar forests. *Aesculus*, distributed in temperate zone, consists of about 25 species. In Hubei Province there is only one species, *Aesculus wilsonii*, and its distribution is limited in western Hubei mountains. There are three species of *Aesculus* in the Carolinas, only one of which is a large tree, *Aesculus octandra*, occurring in the mountains. *Amelanchier* (Rosaceae) is also distributed in the north temperate zone. There are about five species occurring in the Carolinas. *Amelanchier arborea* and its two varieties (var. *laevis* and var. *austromontana*) are widely distributed in the mountainous region. In April and May, their white to pinkish flowers are conspicuous along the mountainsides and in the valleys. In Hubei, there is a single species of *Amelanchier*, *A. sinica*, which is a shrub and is distributed at lower elevations.

The predominant conifers in the mountains of the Carolinas are *Pinus echinata, P. strobus, P. rigida*, and *P. virginiana, Picea rubens*, and *Abies fraseri*.

Generally, the Piedmont region of the Carolinas is comparable to the hilly areas of eastern Hubei, despite the fact that the elevation of the Piedmont is lower than its counterpart in China. In the Piedmont, altitudes vary between 100 and 350 meters, whereas the Dabieshan Mountains in eastern Hubei are about 1,700 meters. The vegetation of both regions is primarily mixed deciduous forest. Important elements of the Piedmont region are *Quercus* (*Q. alba, Q. coccinea, Q. stellata, Q. michauxii*), *Fagus* (*F. grandifolia*), *Carpinus* (*C. caroliniana*), and *Betula* (*B. nigra*). The major deciduous trees in eastern Hubei are: *Quercus* (*Q. variabilis, Q. acutidentata, Q. aliena, Q. dentata*), *Castanea* (*C. mollissima, C. seguinii*), and *Alnus* (*A. trabeculosa*). Of particular interest is the genus *Carya*, which has nine species in the Piedmont, and only one species, *Carya cathayensis*, in Hubei, occurring in eastern hilly region below 1,000 meters.

The Coastal Plain region of the Carolinas is comparable to the Jianghan Plain region of Hubei Province. Both constitute the largest area and lowest elevation of the respective regions under discussion. The obvious difference is the water system: the Carolinian lowland is situated at the eastern border of the Carolinas with immediate connection to the ocean. The lowland in Hubei is located in the middle of the province and is the floodplain of the Changjiang River and its largest tributary, the Han River. The dominant deciduous ligneous plants of these two regions are various oaks; *Quercus chenii* and *Quercus acutissima* frequent in Jianghan Plain region. *Quercus laevis* and *Quercus marilandica* common in the Coastal Plain region. Pines are important components in the lowlands of both areas. In the Jianghan Plain of Hubei the masson pine (*Pinus massoniana*) is dominant, whereas in the Coastal Plain of the Carolinas large areas are covered by six species of pines. They are: the long-leaf pine (*Pinus palustris*), loblolly pine (*P.*-

TABLE 1. A summary of the floras of Hubei and the Carolinas.

	Spermatophytes									
					Angiosperms					
	Pteridophytes		Gymnosperms		Monocots		Dicots		Total	
Categories	Hubei	Carolinas	Hubei	Carolinas	Hubei	Carolinas	Hubei	Carolinas	Hubei	Carolinas
Families	35	16	7	3	23	31	142	130	207	180
Genera	67	30	23	8	169	226	906	687	1,165	951
Species	182	89	37	21	629	940	2,968	2,310	3,816	3,360
Infraspecific taxa	0	0	5	0	0	42	237	132	242	174

nus taeda), pond pine (*Pinus serotina*), short-leaf pine (*Pinus echinata*), slash pine (*Pinus elliottii*), and spruce pine (*Pinus glabra*).

A Comparison of the Floras

The floristic relationship between Hubei and the Carolinas are very close, with comparable number of species, genera, and families. The number of vascular plants of both regions, taken from the Flora Hupehensis (Wuhan Institute of Botany, 1976, 1979) and Radford et al. (1968) are shown in Table 1.

Families that contain more than 20 species of ferns, 10 species of gymnosperms, 25 species of dicotyledons, and 50 species of monocotyledons are given in Table 2.

The floras of the two regions have numerous shared families and genera. Of 207 families of vascular plants in Hubei and 180 in the Carolinas, approximately 75% are represented in both regions. Many of the genera are common to both regions. For example, in *Urticaceae,* there are 15 genera in Hubei; 5 of these are represented in the Carolinas, i.e., *Urtica, Laportea, Boehmeria, Parietaria,* and *Pilea.* In the Betulaceae, *Betula, Alnus, Corylus, Carpinus,* and *Ostrya* are genera common to both floras. In Saxifragaceae, there are 18 genera in Hubei, and 14 in the Carolinas, 10 of which are shared.

Chinese and American botanists have shown that in many genera the species that occur in Eastern Asia and North America are closely related. For instance, in *Buckleya, Phryma, Cornus, Diphylleia,* and *Podophyllum* there are paired species in the floras of Hubei and the Carolinas.

There are, however, some obvious differences between the two floras. First, at the family level, there are 44 families in Hubei not represented in the Carolinas, and 29 families in the Carolinas not occurring in Hubei.

Families in the Hubei flora not in the Carolinas are as follows: Ferns – Angiopteridaceae, Plagiogyriaceae, Gleicheniaceae, Dicksoniaceae, Monachosoraceae, Lindsaeaceae, Sinopteridaceae, Gymnogrammaceae, Parkeriaceae, Loxogrammaceae; Gymnosperms—Ginkgoaceae, Taxaceae, Podocarpaceae, Cephalotaxaceae; Dicots—Piperaceae, Chloranthaceae, Proteaceae, Olacaceae, Balanophoraceae, Tetracentraceae, Eupteleaceae, Cercidiphyllaceae, Sargentodoxaceae, Illiciaceae, Pittosporaceae, Eucommiaceae, Daphniphyllaceae, Coriariaceae, Icacinaceae, Sabiaceae, Elaeocarpaceae, Actinidiaceae, Flacourtiaceae, Stachyuraceae, Begoniaceae, Alangiaceae, Myrtaceae, Trapaceae, Theligonaceae, Myrsinaceae, Pedaliaceae, Gesneriaceae; Monocots—Stemonaceae, Zingiberaceae.

Families in the Carolina flora not in Hubei flora: Ferns—Isoetaceae, Grammitidaceae; Dicots—Annonaceae, Bataceae, Empetraceae, Cactaceae, Diapensiaceae, Cyrillaceae, Sapotaceae, Cabombaceae, Martyniaceae, Elatinaceae, Podostemaceae, Sarraceniaceae, Plumbaginaceae, Dionaeaceae, Turneraceae; Monocots—Bromeliaceae, Arecaceae, Zannichelliaceae, Zosteraceae, Ruppiaceae, Juncaginaceae, Xyridaceae, Mayacaceae, Cannaceae, Marantaceae, Haemodoraceae, Burmanniaceae.

Secondly, in the flora of Hubei the woody elements are more diversified than those of the Carolinas. Based on an incomplete survey, there are about 650 species and varieties, belonging to 200 genera and 73 families, of woody plants native to Hubei. The number of species and varieties of woody plant in the Carolinas flora is 217, belonging to 82 genera and 46 families.

The gymnosperms are much better represent-

TABLE 2. Major families in Hubei and the Carolinas.

Categories	Families	Hubei Genera	Hubei Species & vars.	Carolinas Genera	Carolinas Species & vars.
Ferns	Aspidiaceae	1	(1)	7	24
	Athyriaceae	6	20	(placed in Aspidiaceae)	
Gymnosperms	Pinaceae	8	18	4	14
Dicots	Salicaceae	2	31	2	(13)
	Fagaceae	5	47	3	43
	Polygonaceae	6	72	7	45
	Caryophyllaceae	15	36	17	53
	Ranunculaceae	21	94	16	67
	Berberidaceae	8	48	7	(8)
	Lauraceae	9	54	4	(5)
	Brassicaceae	22	45	26	73
	Saxifragaceae	18	60	14	34
	Rosaceae	31	215	23	117
	Fabaceae	55	131	50	184
	Euphorbiaceae	21	55	11	45
	Aceraceae	2	30	1	(10)
	Rhamnaceae	8	39	5	(5)
	Apiaceae	34	75	36	84
	Ericaceae	7	41	19	70
	Primulaceae	4	47	6	(18)
	Lamiaceae	42	105	34	90
	Scrophulariaceae	25	79	30	85
	Rubiaceae	23	47	11	37
	Caprifoliaceae	10	61	6	28
	Asteraceae	70	306	85	449
Monocots	Poaceae	70	150	93	337
	Cyperaceae	14	120	17	196
	Liliaceae	36	140	35	106
	Orchidaceae	44	104	21	61

ed in Hubei than in the Carolinas. *Metasequoia glyptostroboides* is one of the most outstanding and significant species in the Hubei flora. This relict species was found in western Hubei, where there are about 5,000 very large metasequoia trees growing in a small valley in Lichuan Xian.

Thirdly, each flora has its own endemic and unique genera and species. In Hubei they are: *Saruma* (endemic genus) (Aristolochiaceae), *Tetracentron* (Tetracentraceae), *Sinofranchetia* (Hamamelidaceae), *Bretschneidera* (Bretschneideraceae), *Fortunearia* (Hamamelidaceae), *Hosiea* (Icacinaceae), *Tapiscia* (Staphyleaceae), *Dipteronia* (Aceraceae), *Davidia* (Davidiaceae), and *Emmenopterys* (Rubiaceae). In the Carolinas: *Dionaea* (endemic genus) (Dionaeaceae), *Hexastylis* (Aristolochiaceae), *Houstonia* (Rubiaceae), *Kalmia*, *Leiophyllum*, *Menziesia* (Ericaceae), *Galax* (Diapensiaceae), *Gaylussacia* (Ericaceae), *Sarracenia* (Sarraceniaceae), *Xanthorhiza* (Ranunculaceae), *Ceratiola* (Empetraceae), *Spigelia* (Loganiaceae), and *Conopholis* (Orobanchaceae).

The monotypic genus *Dionaea*, endemic to the Carolinas, is a rare and fascinating perennial known only from the Coastal Plain.

Fourthly, there are also some differences in vegetation types. In western Hubei, at places above 2,000 m, large areas of arrow bamboo (*Sinarundinaria nitida*) forests are common. In the lowland of the Jianghan Plain of Hubei, there are large numbers of aquatic plants, with 100 or more species and varieties.

The unique vegetation of the Carolinas is found on stone outcrops and sandy areas. In some places of the Piedmont, there are areas with rock outcrops, such as 40-Acre Rock, in South Carolina which support many lithophytes, such as *Sedum*

pusillum (Crassulaceae). In the Coastal Plain, extensive sandy areas such as that of Cheraw in South Carolina, support pine forests with *Pinus palustris* as the most common species, and usually not mixed with shrubs. Herbs in sandy areas there are *Amsonia ciliata* (Apocynaceae), *Selaginella arenicola* (Selaginellaceae), and *Opuntia compressa* (Cactaceae). To a visitor from China, the grasslands of the Carolinas are a distinct feature of a landscape not found in Hubei Province.

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Vegetation Map of China

Legend to "Vegetation Map of China"
(1: 14 000 000)

NATURAL VEGETATION

I. Needle-leaved Forests
- (1) Needle-leaved deciduous forests of the cold-temperate zone or on the mountains of the temperate zone.
  - 1. *Larix* forests. a. *L. gnelii.* b. *L. sibirica.*
- (2) Needle-leaved evergreen forests on mountains of the temperate zone.
  - 2. *Picea-Abies-Pinus* forests. a. *Picea-Abies.* b. *Picea.* c. *Pinus.*
- (3) Needle-leaved evergreen woodlands on semi-arid sandy soil of the temperate zone.
  - 3. *Pinus sylvestris* var. *mongolica* woodland.
- (4) Needle-leaved evergreen forests of the temperate zone.
  - 4. *Pinus* forest. a. *P. tabulaeformis.* b. *P. densiflora.*
- (5) Needle-leaved evergreen forests of subtropical or tropical zones.
  - 5. *Pinus armandi* forest.
  - 6. *Pinus massoniana* forest.
  - 7. *Pinus yunnanensis* forest and *P. khasya* forest.
  - 8. *Cunninghamia lanceolata* forest.
- (6) Needle-leaved evergreen forests on mountains of sub-tropical and tropical zones.
  - 9. *Abies-Picea* forest with *Tsuga.*

II. Broad-leaved Forests
- (7) Mixed broad-leaved deciduous and needle-leaved evergreen forests of the temperate zone.
  - 10. Deciduous broad-leaf *Pinus koraiensis* forest.
- (8) Broad-leaved deciduous forests of the temperate and sub-tropical zones.
  - 11. Deciduous oak forest. a. *Quercus mongolica.* b. *Q. liaotungensis.* c. *Q. variabilis, Q. acutedentata, Q. glandulifera.*
  - 12. Mixed forest containing *Acer, Tilia, Fraxinus, Ulmus,* and *Betula.*
  - 13. Mixed forest containing *Pistacia* and trees belonging to Ulmaceae on limestone soil.
- (9) Montane microphyllous deciduous forests of temperate and subtropical zones.
  - 14. *Betula* and *Populus* forest.
- (10) Microphyllous deciduous woodlands of the temperate zone.
  - 15. *Ulmus pumila* woodland on semi-arid sandy soil.
  - 16. *Populus diversifolia* woodland on arid saline meadow soil.
- (11) Mixed broad-leaved deciduous and evergreen forests on limestone soils of the subtropical zone.
  - 17. Mixed forest containing *Platycarya strobilacea, Cyclobalanopsis,* trees belonging to Ulmaceae, etc.
- (12) Mixed broad-leaved deciduous and evergreen montane forests on acid yellow-brown soils of the subtropical zone.
  - 18. Mixed forest containing *Cyclobalanopsis, Castanopsis, Fagus,* etc.
  - 19. Mixed forest containing deciduous broad-leaf trees, evergreen oaks, and *Tsuga.* a. *Cyclobalanopsis glauca, Fagus longipetioloata, Tsuga,* etc. b. *Quercus aquifolioides, Acer, Betula, Tsuga.*
- (13) Broad-leaved evergreen forests of the subtropical zone.
  - 20. Mixed forest containing *Cyclobalanopsis, Castanopsis, Lithocarpus.*
  - 21. Mixed forest containing *Castanopsis,* Lauraceae, Theaceae.
- (14) Broad-leaved evergreen forests of the transitional tropical zone.
  - 22. Mixed forest containing *Castanopsis,* Lauraceae, and Theaceae with some trees belonging to tropical families.
- (15) Broad-leaved evergreen sclerophyllous woodlands or scrubs of the subtropical zone.
  - 23. *Quercus aquifolioides* forest or scrub.
- (16) Tropical broad-leaved semi-evergreen forests (tropical semi-evergreen seasonal forests).
  - 24. Semi-evergreen forest on limestone soil.
  - 25. Semi-evergreen forest on acid lateritic soil.
- (17) Tropical broad-leaved evergreen rain forests.
  - 26. Tropical rain forest.
- (18) Tropical broad-leaved evergreen sclerophyllous forests or scrubs along littoral.
  - 27. Mangrove.

III. Scrub and Coppicelands
- (19) Broad-leaved deciduous scrub of the temperate zone.
  - 28. *Corylus heterophylla, Lespedeza bicolor, Quercus mongolica* scrub.
  - 29. *Ostryopsis davidiana, Spiraea pubescens* montane scrub.
  - 30. *Vitex negundo* var. *heterophylla, Zizyphus jujuba, Cotinus coyggyria* var. *cinera* scrub.
- (20) Mixed broad-leaved evergreen and deciduous scrub on acid soils of subtropical and tropical zones.
  - 31. *Rhododendron, Vaccinium* scrub.
  - 32. *Melastoma, Aporosa* scrub.
- (21) Broad-leaved evergreen succulent scrub on coral islands of the tropical zone.
  - 33. *Scaevala frutescens, S. hainenensis, Pistonia grandis* scrub.
- (22) Broad-leaved evergreen semi-sclerophyllous thickets (shrublands) on the mountains of temperate and subtropical zones.
  - 34. *Rhododendron* scrub.
- (23) Broad-leaved deciduous thickets (alpine shrublands) on the high mountains of temperate and subtropical zones.
  - 35. *Salix* spp., *Dasiphora fruticosa, Caragana jubata* scrub.
- (24) Tundras with evergreen dwarf-shrubs and mosses on high mountains in the temperate zones.
  - 36. Montane tundra containing *Salix roundifolia, Vaccinium vitisidaea,* etc.
- (25) Alpine deciduous cushion sub-shrubs mixed with herbs, combined with alpine sparse vegetation of temperate and subtropical zones.
  - 37. *Arenaria musiformis, Androsace tapete* cushion-like vegetation.

IV. Deserts and Xerophytic Shrubs
- (26) Temperate deciduous dwarf sub-shrub deserts.
  - 38. *Sympegma regelii* rocky desert.
  - 39. *Anabasis* gravelly desert.
  - 40. *Reaumuria soongarica* gravelly desert.
  - 41. *Artemisia* loamy desert with ephemeral forbs.
- (27) Temperate succulent halophytic dwarf sub-shrub deserts.
  - 42. *Kalidium* saline desert.
- (28) Temperate shrub and sub-shrub deserts.
  - 43. *Ephedra przewalskii, Zogophyllum xanthoxylum, Nitraria sphaerocarpa, Calligonum* spp. gravelly desert.
  - 44. *Caragana tibetica, Ceratoides latens* sandy gravelly desert.
  - 45. *Potaninia mongolica, Ammopitanthus mongolicus, Tetraena mongolica* sandy gravelly desert.
  - 46. *Artemisia sphaerocephalla, A. ordosica* sandy desert.
  - 47. *Calligonum* sandy desert.
  - 48. Sandy desert with sparse *Tamarix.*
- (29) Temperate semi-arboreal deserts (Saksaoul communities).
  - 49. *Haloxylon persicum, H. ammodendron* sandy desert.
  - 50. *Haloxylon ammodendron, Reaumuria soongarica* loamy desert.
  - 51. *Ephedra przewalskii, Haloxylon ammodendron.*
- (30) Cold high-mountain deserts with creeping or matted dwarf sub-shrubs of the temperate zone.
  - 52. [illegible]*toides compacta, Ajania tibetica* sandy grav-

V. Steppes and Savannas
- (31) Temperate forb-grass steppes mesoxerophytic steppes or meadow steppes.
  - 53. *Aneurolepidium chinense* steppe.
  - 54. *Filifolium sibiricum* steppe.
  - 55. *Bothriochloa ischaemum, Themeda triandra* var. *japonica* steppe with richness of forbs.
- (32) Temperate needlegrass steppes.
  - 56. *Stipa grandis, S. krylovii* steppe.
  - 57. *Stipa bungeana, S. breviflora* steppe.
  - 58. Temperate montane needlegrass steppe.
- (33) Temperate dwarf-shrub or sub-shrub needlegrass steppes.
  - 59. *Stipa gobica* steppe. a. with *Artemisia frigida.* b. with *Stipa glareosa, Artemisia xerophylla.*
  - 60. *Stipa breviflora, Ajania fruticulosa* steppe.
  - 61. Montane dwarf-shrub or dwarf sub-shrub needlegrass steppe.
- (34) High-mountain steppes of temperate and subtropical zones.
  - 62. Forb, *Poa, Festuca* steppe.
  - 63. *Stipa purpurea* steppe. a. with *Stipa subsessiliflora* var. *basiplumosa.* b. with *Festuca pseudoovina.*
  - 64. *Stipa subsessiliflora* var. *basiplumosa, Ceratoides compacta* steppe.
- (35) Subtropical and tropical savannas.
  - 65. *Heteropogon contortus, Cymbopogon distans* savanna with thorny scrub.

VI. Meadow and Swamp Vegetation
- (36) Temperate meadows.
  - 66. Graminoid, forb meadow.
  - 67. Halophytic grass and forb meadow.
- (37) Alpine and subalpine meadows, locally combined with scrub in temperate and subtropical zones.
  - 68. *Kobresia pygmaea, K. tibetica* meadow.
  - 69. Grass, forb, *Carex* meadow.
  - 70. Halophytic grass, forb, *Kobresia* meadow.
- (38) Temperate graminoid swamp.
  - 71. *Phragmites communis, Carex rhynchophysa* swamp.
- (39) High-mountain graminoid swamps of temperate and subtropical zones.
  - 72. *Carex, Kobresia* swamp.

CULTURAL VEGETATION

I. One crop annually, cold-resistant economic crops.
  - 73. Spring wheat, soybean, corn, millet, sugar beet, flux.
  - 74. Spring wheat, millet, potatoes, sugar beet, flux.
  - 75. Spring barley, spring wheat, pea, potatoes, rapeseed.

II. Two crops annually or three crops in two years (with rice locally).
  - 76. Winter wheat, soybean, corn, peanut, sweet potatoes, tobacco, apple, pear, grape.
  - 77. Winter wheat, kaoliang, corn, millet, three crops in two years; soybean, cotton, Chinese date, apple, pear, grape, persimmon, chestnut, walnut.
  - 78. Winter (spring) wheat, corn, millet, three crops in two years or two crops annually; cotton, grape, Hami melon, pear, apricot.

III. Two crops containing upland and rice annually; subtropical evergreen and deciduous economic forest and orchard.
  - 79. Summer rice, winter wheat (rapeseed) two crops annually; cotton, peanut, tea, pomegranate, peach, pear, loquat.
  - 80. Summer (corn), winter wheat (rapeseed), two crops annually; potatoes, tobacco, tea, lacquer, red bayberry, walnut, apple, pear.

IV. Double-cropping rice followed by a cool-loving crop annually or three upland crops annually, and subtropical evergreen economic forest and orchard.
  - 81. Double-cropping rice followed by winter wheat (rapeseed) or green manure; cotton, ramie, mulberry, orange.
  - 82. Single or double-cropping rice followed by winter wheat (rapeseed) annually; sweet potatoes, peanut, grains, five crops in two years; sugarcane, ramie, orange, tung oil, mulberry, palm.
  - 83. Single or double-cropping rice followed by winter wheat, rapeseed, green manure annually, or sweet potatoes, grains, soybean, three upland crops annually, ramie, jute, tea, tea oil, red bayberry, orange, loquat.

V. Double-cropping rice followed by warm-loving crops, and tropical evergreen economic forest, orchard.
  - 84. Double-cropping rice followed by sweet potatoes, double-cropping corn, sugarcane, manioc, litchi, longan, banana, pineapple.
  - 85. Double-cropping rice, winter peanut, sugarcane, vanilla, sisal, rubber, coconut, coffee.

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Systematics Symposia Published

In 1953 the Missouri Botanical Garden began holding a series of annual systematics symposia each fall. Since 1969, with the sixteenth symposium, the Garden has published the proceedings of most in its quarterly series, ANNALS OF THE MISSOURI BOTANICAL GARDEN. Those published symposia which are available are listed below, and the price of all except the twenty-fourth is $10.00. The twenty-fourth, which was reprinted separately from the ANNALS, is available for $6.00. Many of these symposium issues of the ANNALS contain other papers, but each issue listed below contains the complete proceedings of the particular symposium. The proceedings of the 1981 symposium will be published during the second half of 1982, and if you wish to purchase a copy of that symposium, you may subscribe at this time. Upon publication, your copy will be sent.

Sixteenth Annual Symposium, 1969—TROPICAL ISLAND BIOGEOGRAPHY. 56(3). 127 pp. $10.00.

Seventeenth Annual Symposium, 1970—HYBRIDIZATION, EVOLUTION, AND SYSTEMATICS. 59(3). 142 pp. $10.00.

Twentieth Annual Symposium, 1973—PLANT-ANIMAL COEVOLUTION. 61(3). 132 pp. $10.00.

Twenty-first Annual Symposium, 1974—BIOGEOGRAPHY. 62(2). 143 pp. $10.00.

Twenty-second Annual Symposium, 1975—EVOLUTION AT THE POPULATION LEVEL. 63(2). 100 pp. $10.00.

Twenty-third Annual Symposium, 1976—CHEMOSYSTEMATICS. 64(2). 98 pp. $10.00.

Twenty-fourth Annual Symposium, 1977—SYSTEMATICS STUDIES IN AFRICA. 223 pp. $6.00.

Twenty-fifth Annual Symposium, 1978—PALYNOLOGY AND SYSTEMATICS. 66(4). 248 pp. $10.00.

Twenty-sixth Annual Symposium, 1979—EVOLUTION AND SYSTEMATICS OF THE GRAMINEAE. 68(1). 104 pp. $10.00.

Twenty-seventh Annual Symposium, 1980—REPRODUCTIVE STRATEGIES IN PLANTS AND ANIMALS. 68(2). 146 pp. $10.00.

Twenty-eighth Annual Symposium, 1981—BIOLOGICAL STUDIES IN CENTRAL AMERICA. 69(3). 304 pp. $15.00.

Twenty-ninth Annual Symposium, 1982—BIOGEOGRAPHICAL RELATIONSHIPS BETWEEN TEMPERATE EASTERN ASIA AND TEMPERATE EASTERN NORTH AMERICA. 70(3 & 4). 327 pp. and map. $15.00.

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CORNUS KOUSA

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ON THE SIGNIFICANCE OF PACIFIC INTERCONTINENTAL DISCONTINUITY

WU ZHENGYI[1]

The abundant disjunctions in the ranges of plant families and genera in Eastern Asia and temperate North America is one of the most familiar and important patterns of discontinuity in all of biology. From the time Asa Gray (1859) drew special attention to these discontinuities in range over a century ago, they have been studied and discussed by many authors (e.g., Li, 1952; Good, 1974; Graham, 1972; Wood, 1972). Formerly, it was believed that there were only about 80 genera of plants with such ranges, but now it is known that there may actually be more than 120, of which 117 are recorded from China (see Appendix 1). These genera comprise about 4% of the total number of genera of higher plants (2,980) in the entire Chinese flora. They belong to 60 families, mostly temperate in distribution; some of these families are primarily tropical and subtropical in distribution, however. Woody families that include trees or shrubs are listed in Table 1.

In all, there are 45 genera distributed among 28 families of which four (Illiciaceae, Calycanthaceae, Nyssaceae—sensu stricto, and Styracaceae) exhibit the same sorts of disjunctions in range as the genera they include. The same pattern—with familial and generic disjunctions approximately parallel—is exhibited by families composed of herbaceous plants (Nelumbonaceae, Saururaceae, Phrymaceae, Croomiaceae). To these families perhaps should be added Schisandraceae, which exhibits a similar pattern of distribution. All of them are disjunct between eastern Asia and eastern North America, although Nelumbonaceae extends through the tropics to northern Australia, and Illiciaceae, Schisandraceae, and Nyssaceae extend to the West Indies and to southeast Asia. Styracaceae have a range similar to that of Hydrangeaceae sensu stricto, and might be derived from the latter through genera such as *Deutzia*. A single species of *Styrax* extends from eastern Asia to the Mediterranean region. For Hydrangeaceae, *Hydrangea* and *Deutzia* range through the mountains of Mexico and the Andes to Chile.

In agreement with Good (1974), I believe that many of these genera could be survivors of an ancient flora that failed to persist in Europe and western Asia. I do not agree with Good, however, that these plants can appropriately be regarded as "circumboreal" in distribution. Rather, I believe that they might be relicts of a warm temperate to subtropical montane flora derived from a Tertiary Paleotropical flora that was present on the mountains in warm-temperate to subtropical climates in the Old World in early Tertiary or perhaps late Cretaceous time. The persistence of such ancient patterns of distributions is suggested, among other lines of evidence, by the extension of some of these genera far southward into the tropics or even to the lands of the Southern Hemisphere; even in these cases, however, the centers of distribution are definitely in North America and temperate Eastern Asia.

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TABLE 1. Families with trees or shrubs.

	Number of Genera
Taxaceae (*Torreya*)	1
Pinaceae (*Pseudotsuga, Tsuga*)	2
Cupressaceae (*Calocedrus, Chamaecyparis, Thuja*)	3
Magnoliaceae (*Liriodendron, Magnolia*)	2
Illiciaceae (*Illicium*)	1
Lauraceae (*Sassafras*)	1
Berberidaceae (*Mahonia*)	1
Calycanthaceae (*Calycanthus*)	1
Theaceae (*Gordonia, Stewartia*)	2
Iteaceae (*Itea*)	1
Hydrangeaceae (*Decumaria, Hydrangea*)	2
Rosaceae (*Photinia, Physocarpus, Sorbaria,* and 2 herbaceous genera)	3(–5)
Caesalpiniaceae (*Gleditsia, Gymnocladus*)	2
Papilionaceae (*Lespedeza* and 4 herbaceous genera)	1(–5)
Buxaceae (*Pachysandra*)	1
Hamamelidaceae (*Hamamelis, Liquidambar*)	2
Santalaceae (*Buckleya, Pyrularia*)	2
Rhamnaceae (*Berchemia*)	1
Anacardiaceae (*Toxicodendron*)	1
Juglandaceae (*Carya*)	1
Cornaceae (*Bothrocaryum* = *Cornus* sect. *Thelycrania*)	1
Nyssaceae (*Nyssa*)	1
Araliaceae (*Aralia, Oplopanax,* and herbaceous *Panax*)	2(–3)
Ericaceae (*Leucothoe, Lyonia, Pieris, Therorhodion,* and *Hugeria*)	5
Styracaceae (*Halesia*)	1
Oleaceae (*Chionanthus* s.s., *Osmanthus*)	2
Rubiaceae (*Cephalanthus* and 2 herbaceous genera)	1(–3)
Caprifoliaceae (*Symphoricarpos* and 1 herbaceous genus)	1(–2)
TOTAL 28 families	45 genera

Among the genera listed in Appendix 1, some of the monotypic ones (including *Glehnia* of Umbelliferae, *Phryma* of Phrymataceae, *Symplocarpus* of Araceae, *Diarrhena* and *Schizachne* of Gramineae) belong to two distinct categories of distribution. *Phryma*, for example, appears to be one of the relictual representatives of the Tertiary flora previously mentioned. It has a typical pattern of disjunction between eastern Asia and eastern North America. In contrast, *Glehnia, Symplocarpus, Diarrhena,* and *Schizachne* (for a discussion of *Schizachne* and *Diarrhena* see Koyama & Kawano, 1963) might actually have a Beringian distribution and might therefore be direct decendents of the flora that was common to northeastern Asia and Pacific North America when migration through Beringia was still quite possible in the middle Tertiary. This latter group of genera might be considered "circumboreal" in distribution and, in some cases (*Schizachne*) might have been distributed throughout Arctic Europe by way of northeastern Siberia and Japan, temperate North America, and even the mountainous regions of the western United States. Genera of this group appear to be "younger" in their distribution than *Phryma*, and their pathway of distribution can be regarded as very obvious.

Other oligotypic genera mentioned in Appendix 1 can be analyzed as follows. First, three families and six genera of conifers are common in eastern Asia and North America. Among them, *Pseudotsuga, Tsuga,* and *Chamaecyparis,* although not oligotypic, might still dominate in forests in these regions like the oligotypic genera *Torreya, Thuja,* and *Calocedrus. Calocedrus* has a range that extends through northern Burma and northeastern Thailand, and southwestern China to Hainan and Taiwan (two species) and then reappears in the Pacific region in North America as a single species. Such a distribution, taken together with the fact that its close relatives are found in the Southern Hemisphere [i.e., *Libocedrus* with three species in New Caledonia and two species in New Zealand; *Papuacedrus* from New Guinea to the Moluccas (Li, 1953)], suggests that the range disjunction of *Calocedrus* might have originated as a result of a Gondwanan distribution that extended through the Southern Hemisphere.

The remaining genera number no fewer than 35 that have either two or three species. Paired species occur in many oligotypic genera and have been fully discussed by Li (1952). Among the better known of these are *Liriodendron* (Magnoliaceae), *Nelumbo* (Nelumbonaceae), *Achlys* and *Caulophyllum* (both Podophyllaceae), *Menispermum* (Menispermaceae), *Saururus* (Saururaceae), *Stylophorum* (Papaveraceae), *Adlumia* (Fumariaceae), *Decumaria* (Hydrangeaceae), *Chionanthus* (Oleaceae), and *Campsis* (Bignoniaceae). Genera with three species are not as richly

FIGURE 1. The distribution of *Torreya*.

FIGURE 2. The distribution of *Pachysandra*.

FIGURE 3. The distribution of *Carya*.

represented as those with two species. Among them are many that have two species in eastern Asia and one in North America, like *Calocedrus*; similar patterns occur in *Diphylleia* (Podophyllaceae), *Boschniakia* (Orobanchaceae), and *Tulotis* (Orchidaceae), among others. The corresponding pattern with two species in North America and one in Asia occurs, for example, in *Zizania* (Gramineae). Of these oligotypic genera it can be said that the species are obviously closely related in every case and that in general they represent either primitive families or relatively primitive lines within phylogenetically advanced families. It is clear that they constitute relicts in every sense of the word. Magnoliaceae, one of the more ancient families of dicotyledonous plants, has in general a distribution pattern that can be represented by that of the genus *Magnolia*. In general, the family is disjunct between eastern Asia and North America but extends south in the mountains into tropical southeast Asia and to South America. *Liriodendron*, on the other hand, is strictly an eastern Asian-eastern North American genus confined to temperate and subtropical zones. The western limit of *Liriodendron* in China extends to southeastern and northeastern Yunnan, where many other relict genera such as *Rhoiptelea*, *Diplopanax*, *Annamocarya*, and *Davidia* are also known. *Liriodendron* also extends to the northern part of Viet Nam where the most primitive species of *Platanus* (*P. kerrii*, with unlobed leaves and pinnate venation) exists, as well as to adjacent mountains of southeastern Yunnan. In view of these distribution patterns it can be hypothesized that both Magnoliaceae and Platanaceae originated in the subtropical mountains of southeastern Asia.

Although the theories that formerly placed Nelumbonaceae as an ancestor of the monocots have now largely been discarded, this family certainly represents a very ancient lineage that has been in existence for a very long time both in Asia and in America; it might represent a survivor of the floras that existed in both areas in the early Tertiary and Late Cretaceous times. The same appears to be true of many of the other genera discussed here. Among the families Ranunculaceae, Paeoniaceae, Berberidaceae, and Podophyllaceae, there are at least four bispecific or trispecific genera that are disjunct between eastern Asia and eastern North America. Among them, *Jeffersonia* is now occasionally divided into two genera, with the Asian species placed in the genus *Plagiorhegma*. *Podophyllum* is represented by two closely allied, segregate genera, *Sinopodophyllum* and *Dysosma*, which have three to nine species in China but a single species referred to *Podophyllum* sensu stricto in North America. Both are obviously derived from an ancient *Podophyllum*-like stock while *Ranzania*, a monotypic endemic of Japan (Ohwi, 1965), obviously is another relict genus ultimately derived from the same stock.

Another very interesting small family is the Saururaceae; it has a strictly eastern Asian-eastern North American disjunct distribution. Both paired genera (*Houttuynia* and *Anemopsis*) and paired species (*Saururus chinensis* and *S. cernua*) are represented among the four genera and six species of the family. This family certainly originated in the subtropical region during the Late Cretaceous and early Tertiary. Among the members of this family, *Houttuynia* occurs from the Himalayas to Japan; *Anemopsis* in Mexico and the southwestern United States; *Saururus* from the Philippines and Indochina through the Yangtze Valley; and *Gymnotheca* with two closely allied species of scattered distribution in southeastern Yunnan, Guangxi, Guizhou, and Sichuan. *Saururus* is morphologically and geographically quite similar to *Zippelia* ("*Circaeocarpus*") of the Piperaceae, a large pantropical family that appears to be ultimately of Gondwanan distribution. The possible relationship between the *Saururus* and *Zippelia* should be investigated further.

Menispermum, which has many perianth segments that are irregularly spirally arranged and more than four whorls of stamens, is one of the most primitive members of the mainly tropical and subtropical Menispermaceae. It is the only member of this family that has a disjunction in range between eastern Asia and temperate North America, which suggests that *Menispermum* could be an ancient relict derived from subtropical mountains in Laurasia. It might be close to the ancestral form of this now primarily tropical family.

The genus *Penthorum* (Penthoraceae) can be regarded as intermediate between the Crassulaceae and Saxifragaceae. Its disjunct distribution pattern coincides with its primitive morphology and critical phylogenetic position. Similar statements could be made for *Tiarella* (Saxifragaceae) and *Decumaria* (Hydrangeaceae).

Other primitive families such as Hamamelidaceae, Altingiaceae, Cornaceae, Araliaceae, and the more primitive tribes in some large families, such as Sophoreae of the Papilionaceae (*Cladrastis*), also are represented in the disjunct eastern

FIGURE 4. The distributions of *Camptotheca* (horizontal lines) and *Nyssa* (vertical lines).

FIGURE 5. The distributions of *Buckleya* (dashed outline), *Decumaria* (vertical lines), *Stylophorum* (horizontal lines), and *Symphoricarpos* (shaded).

FIGURE 6. The distributions of Illiciaceae: *Illicium* (vertical lines); and Schisandraceae: *Kadsura* (dashed outline) and *Schisandra* (horizontal lines).

FIGURE 7. The distributions of Calycanthaceae: *Calycanthus* (vertical lines) and *Chimonanthus* (shaded).

FIGURE 8. The distribution of *Nelumbo*.

FIGURE 9. The distributions of Magnoliaceae (shaded): *Liriodendron* (solid) and *Magnolia* (vertical lines).

Asian-eastern North American pattern of distribution. It seems clear that they, too, are derived from the ancient flora that is being discussed here.

There are a number of phylogenetically more advanced families that exhibit similar disjunction in range. These include Rubiaceae, Campanulaceae, Scrophulariaceae, Bignoniaceae, Phrymaceae, and Labiatae of the Sympetalae, as well as Cyperaceae, Gramineae, and Orchidaceae among the monocots. The fact that such advanced families share a similar disjunction in range might be taken as evidence that some angiosperm families are older than currently believed.

Following this review of a few of the oligotypic genera that are represented both in Asia and in North America, we now pass on to consider some of the genera represented by more species in one or both areas. Among them are *Illicium* (Illiciaceae) and *Schisandra* (Schisandraceae), which have been extensively studied by Smith (1947).

A variant of this sort of distribution is one with a disjunction in range between eastern Asia and Mexico-Central America. *Abelia* (Caprifoliaceae), for example, has 10 to 14 species widely distributed in the forested half of China. In the Western Hemisphere it is represented by two species that occur only in Mexico. *Cleyera* (Ternstromiaceae), in contrast, has a distribution that centers in Mexico, extends to Panama and the West Indies, but is represented in Asia by a single species that ranges from south of the Yangtze Valley to Japan. *Deutzia* (Hydrangeaceae) and *Distylium* (Hamamelidaceae) are similar in their distribution, but in these cases differentiation of the Eastern and Western Hemisphere elements have proceeded so far that they must be regarded as pairs of genera: *Deutzia-Neodeutzia*; *Distylium-Molinadendron*. Paired genera that collectively represent disjunct ranges between Asia and North America are listed in Appendix 2. A surprisingly close relationship between the floras of China and Mexico has been detected recently by van Beusekom (1971), who regards *Meliosma alba* as common to these very widely separated regions.

Moving farther south, I would like to point out that there also is a pattern of disjunction in the ranges between tropical Asia and tropical America. About 37 genera are common to these very distant regions and they could represent a very early pattern of disjunction in range. Among the families represented primarily by trees and shrubs are genera such as *Talauma* (Magnoliaceae), *Anaxagorea* (Annonaceae), *Litsea, Nothaphoebe, Persea,* and *Phoebe* (Lauraceae), *Hedyosmum* (Chloranthaceae), *Eurya* (Ternstroemiaceae), *Saurauia* (Saurauiaceae), *Sloanea* (Elaeocarpaceae), *Microtropis* (Celastraceae), *Pristimera* (= *Reissantia*) (Hippocrateaceae), *Sageretia* (Rhamnaceae), *Picrasma* (Burseraceae), *Sapindus* (Sapindaceae), *Meliosma* (Meliosmaceae), *Turpinia* (Staphyleaceae), *Allospondias* and *Spondias* (Anacardiaceae), and *Gaultheria* (Ericaceae). Many of these genera are common or even dominant in the tropical and subtropical evergreen forests that extend from southeastern Tibet to Taiwan in China. They can also be regarded as descendents of the sort of vegetation that seems to have predominated in the subtropical mountains of the Northern Hemisphere in the Late Cretaceous and the early Tertiary.

Juglandaceae presents an interesting example of the differentiation of these warm temperate to tropical northern floras (Lu, 1980). *Annamocarya,* which extends from tropical Indochina into southwestern China, is very likely to be near the common ancestor of *Carya,* which is disjunct in distribution in eastern Asia and eastern North America. It is distributed in eastern Asia from northern Viet Nam to the southern part of the Yangtze Valley. *Pterocarya* and *Platycarya,* in contrast, are mainly eastern Asian, with *Platycarya* extending west of the Caucasus; *Cyclocarya* is endemic to China, but known from the fossil record in the Paleogene of North America (Manchester & Dilcher, 1982); *Juglans,* which also appears to be a relict from the Late Cretaceous, is widely distributed, ranging in Asia south to Indochina and in the Western Hemisphere from Canada to Cuba and through Central America to Andean South America. *Juglans* might be closely related to an ancestral species of Juglandaceae. *Engelhardtia,* which is a genus of southeastern Asia that extends northward to the Nanling Mountains of south China, is a genus paired with *Oreomunnea,* represented by three species in Mexico and Central America.

Another family that can be hypothesized to have originated in the mountains of the subtropical regions of the Northern Hemisphere, like the Juglandaceae, is the Chloranthaceae. The present distribution of this small family can be characterized as primarily tropical and subtropical, but when its distribution is examined in detail, it appears that it can best be regarded as being of Gondwanic origin (see also Raven &

FIGURE 10. The distributions of Saururaceae: *Anemiopsis* (shaded), *Gymnotheca* (solid), *Houttuynia* (vertical lines), and *Saururus* (horizontal lines).

FIGURE 11. The distributions of Juglandaceae: *Annamocarya* (solid), *Carya* (horizontal lines), *Engelhardtia* (dashed outline), *Juglans* (shaded), *Oreomunnea* (diagonal lines), *Platycarya* (heavy outline), and *Pterocarya* (vertical lines).

FIGURE 12. The distributions of *Castanopsis* (vertical lines) and *Lithocarpus* (horizontal lines).

Axelrod, 1974). The relatively close relationship between *Ascarina* (with eight species from Malaysia and Polynesia, including New Zealand) and *Ascarinopsis* (a monotypic genus of Madagascar) suggests that these genera differentiated when migration between Australasia and Africa was much easier than it is at present. *Hedyosmum,* on the other hand, is very well developed with about 40 species in tropical America and the West Indies, and one in the Old World, where it occurs from Sumatra and Borneo northward to Hainan in southern China. The most primitive member of Chloranthaceae surviving at the present time, however, is certainly *Sarcandra,* which is one of the very few angiospermous genera that lacks vessels. Overall, *Sarcandra* is relatively closely related to *Chloranthus* and occurs with that genus from tropical southeastern Asia northward through eastern Asia. *Chloranthus* extends further north to the mixed forest in northeastern China and is clearly of Late Cretaceous origin.

Similar floristic connections between tropical Asia and tropical America are found among more advanced families such as Compositae. Thus, *Gochnatia* (= *Leucomeris*) is a woody genus of this family that has about 64 species extending from the southern United States through Mexico and the West Indies to South America; but it is also represented by two species that have a discontinuous distribution in the Himalayas and southeastern Asia. One of these Asian species occurs in Nepal and the other ranges from Pegu-Burma to southwestern Yunnan and the upper Yangtze Valley between Yunnan and Sichuan. *Gochnatia,* together with the monotypic and endemic genus *Nouelia* that occurs in the same part of Asia, is a small tree belonging to the tribe Mutisieae, perhaps the most primitive of the family Compositae. In the tribe Mutisieae, there are many woody genera that appear to be primitive in their characteristics and occur in Central and South America and in Africa, where they are well represented both in the tropical regions and in the southern, more temperate portions. Mutisieae certainly appear to be of Gondwanic origin.

The two members of Mitrastemonaceae recently discovered in Yunnan and Fujian on the mainland of China are extremely interesting. *Mitrastemon* is represented by one species in Japan (Ohwi, 1965), and one or two species in Taiwan (Liu & Lai, 1976) (one of which extends to Fujian), one species from Indochina and southeastern Yunnan, one species in Borneo, and one species in Sumatra, with an additional two species completely isolated from their Asian relatives in Mexico (Matuda, 1947) and Central America. In southeastern and temperate eastern Asia, every species of this genus is, without exception, a root parasite of *Castanopsis. Castanopsis* is a dominant genus that forms extensive forests in the subtropical to tropical mountains from which so many of the genera discussed in this paper are derived. If *Castanopsis* ever occurred in the New World, it is now extinct, but it has been replaced during the course of evolution by the related genus *Chrysolepis,* which consists of two species in California and Oregon. Despite the absence of *Castanopsis* and related genera in Mexico and Central America, Mitrastemonaceae, which are parasites of this genus in Asia, have persisted in a more depleted vegetation than has survived in Asia.

I would now like to summarize with a few general conclusions derived from the preceding discussion:

(1) The discontinuity in plant range that spans the Pacific Ocean is a very important one for the study of floristic evolution.

(2) The eastern Asian-eastern temperate North American, and the tropical Asian-tropical American disjunctions both appear to have been derived from similar ancestral floras and are closely related to the tropical southeastern (Indo-Malayan) and temperate eastern (including Sino-Japanese and Sino-Himalayan) Asian elements.

(3) All of these disjunctions in range seem to have been derived from the same upper Cretaceous and lower Tertiary paleotropical flora that occurred on the mountains within the tropical to subtropical zones (Axelrod, 1952, 1960).

(4) The pattern of these disjunctions is consistent with an origin of some of the constituent groups of angiosperms in the Late Cretaceous or even earlier (Axelrod, 1961).

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APPENDIX 1. Eastern Asia and eastern North America intercontinental discontinuities.

Family	Genus	Number of Species in E. Asia/ N. Am.	Distribution in E. Asia	Distribution in N. Am.
Cupressaceae	*Calocedrus* (*Heyderia*)	2/1	S to N Burma, NE Siam	Pacific N. Am.
Cupressaceae	*Chamaecyparis*	3/3	S to Taiwan	
Cupressaceae	*Thuja*	3/2		
Pinaceae	*Pseudotsuga*	5/2		W N. Am.
Pinaceae	*Tsuga*	5–10/2		
Taxaceae	*Torreya*	5/2		Florida and California
Anacardiaceae	*Toxicodendron*	18+/8		S to S. Am.
Apocynaceae	*Amsonia*	1/17		N. Am.
Apocynaceae	*Trachelospermum*	10/1		SE United States
Araliaceae	*Aralia*	30+/4+	S to Indo-Malaya	
Araliaceae	*Oplopanax*	1/1		
Araliaceae	*Panax*	7/2		
Berberidaceae	*Mahonia*	40+/30−	S to Sumatra	S. Am.
Bignoniaceae	*Campsis*	1/1		S to W. Indies
Bignoniaceae	*Catalpa*	7/4		S to W. Indies
Buxaceae	*Pachysandra*	3/1		E United States
Caesalpiniaceae	*Gleditsia*	10/2	Tropical Africa	S to S. Am.
Caesalpiniaceae	*Gymnocladus*	3/1	S to Assam, Burma	
Calycanthaceae	*Calycanthus*	1/1		SW and E United States
Campanulaceae	*Heterocodon*	1/1		W N. Am.
Caprifoliaceae	*Symphoricarpos*	1/15		
Caprifoliaceae	*Triosteum*	3–6/4–5		
Compositae	*Brachyactis*	4/1	N Asia	N. Am.
Compositae	*Cacalia*	±60/4		N. Am. + and S to S. Am.
Compositae	*Crossostephium*	1+3/1		California
Cornaceae	*Bothrocaryum* (*Cornus* sect. *Thelycrania*)	1/1		NE Am.
Penthoraceae	*Penthorum*	1/1	S to Indochina	Atlantic N. Am.
Diapensiaceae	*Shortia*	4–8/1		SE United States
Ericaceae	*Leucothoe*	4/3(–40)		S to S. Am.
Ericaceae	*Lyonia*	9/21	S to Himalayas	W. Indies
Ericaceae	*Pieris*	6/2		
Ericaceae	*Therorhodion*	1/2	NE Asia	NW Am.
Ericaceae	*Hugeria*	2/1		
Iteaceae	*Itea*	12/1	S to W. Malaysia	Atlantic N. Am.
Fagaceae	*Castanopsis* (incl. *Chrysolepis*)	60–100/2	S to tropical Asia	W United States
Fumariaceae	*Adlumia*	1/1	NE Asia	E N. Am.
Fumariaceae	*Dicentra*	2+1/10–11		
Hamamelidaceae	*Hamamelis*	1+/2		E N. Am.
Hamamelidaceae	*Liquidambar*	2+1/3	SW Asia Minor	Atlantic N. Am.
Hydrangeaceae	*Decumaria*	1/1	S to Indochina	
Hydrangeaceae	*Hydrangea*	45/35+	S to Philippines, Java	Atlantic N. Am., Chile
Illiciaceae	*Illicium*	21+/	S to W. Malaysia	Mexico, W. Indies
Juglandaceae	*Carya*	2/23	S to Indochina	E N. Am.
Labiatae	*Agastache*	1/20		S to Mexico
Labiatae	*Meehania*	5/1	sp. complex	E United States
Loganiaceae	*Gelsemium*	1/2	S to N Borneo, Sumatra	N Mexico

Appendix 1. (Continued).

Family	Genus	Number of Species in E. Asia/ N. Am.	Distribution in E. Asia	Distribution in N. Am.
Magnoliaceae	*Liriodendron*	1/1	S to N Indochina	
Magnoliaceae	*Magnolia*	30+/5+	S to Java	Venezuela
Menispermaceae	*Menispermum*	1/2		Atlantic N. Am., S to Mexico
Monotropaceae	*Hypopitys*	1/1	S to Himalaya	Colombia
Nelumbonaceae	*Nelumbo*	1/1	NE Australia	S to Colombia
Nyssaceae	*Nyssa*	6/4	S to W Malaysia	E N. Am.
Oleaceae	*Chionanthus* s.s.	1/2		E N. Am.
Oleaceae	*Osmanthus*	15/3	S to SE Asia	
Orobanchaceae	*Boschniakia*	2/1		NW N. Am.
Papaveraceae	*Stylophorum*	2/1		Atlantic N. Am.
Papilionaceae	*Amphicarpaea*	2–3+1/1	S. Africa	?S to tropical Am.
Papilionaceae	*Apios*	6/4		
Papilionaceae	*Cladrastis*	4/1		E N. Am.
Papilionaceae	*Lespedeza*	65+/15–30	S to Australia	
Papilionaceae	*Thermopsis*	7/23		E United States
Papilionaceae	*Wisteria*	7/3		E N. Am.
Phrymaceae	*Phryma*	1/1		
Podophyllaceae	*Achlys*	1/1		Pacific N. Am.
Podophyllaceae	*Caulophyllum*	1/1		
Podophyllaceae	*Diphilleia*	2/1		Atlantic N. Am.
Podophyllaceae	*Jeffersonia*	1/1		
Podophyllaceae	*Podophyllum*	1/1		E N. Am.
Polygonaceae	*Antenoron*	2–3/1	S to Philippines	
Ranunculaceae	*Enemion* (*Isopyrum*)	1/1–3		
Rhamnaceae	*Berchemia*	13+/1–2	S to tropical Africa	Atlantic N. Am.
Rosaceae	*Acomastylis*	1/12		
Rosaceae	*Photinia*	40/20	S to Sumatra	
Rosaceae	*Physocarpus*	1/9–10	NE Asia	
Rosaceae	*Sieversia*	1/1	NE Asia	Aleutian Isl.
Rosaceae	*Sorbaria*	5+/1	?W to central Asia	
Rubiaceae	*Cephalanthus*	1+1/5	Africa	to warm Am.
Rubiaceae	*Kelloggia*	1/1	Yunnan-Tibet	SW United States
Rubiaceae	*Mitchella*	1/1	NE Asia	Atlantic N. Am.
Santalaceae	*Buckleya*	2/1		S United States
Santalaceae	*Pyrularia*	2/2	S to Himalaya	SE United States
Saururaceae	*Saururus*	1/1	S to Philippines	E United States
Saxifragaceae	*Astilbe*	15/2		
Saxifragaceae	*Mitella*	2/12		
Saxifragaceae	*Tiarella*	1/6		Pacific and Atlantic N. Am.
Schisandraceae	*Schisandra*	17/1	S to tropical Asia	
Scrophulariaceae	*Castilleja*	1/30–200		N. Am. to S. Am.
Scrophulariaceae	*Orthocarpus*	1/25–30		W Am.
Scrophulariaceae	*Veronicastrum* s.s.	1/1	NE Asia	temperate NE N. Am.
Solanaceae	*Leucophysalis* (= *Physaliastrum*)	4/1		
Styracaceae	*Halesia*	1/3		SE United States
Theaceae	*Gordonia*	8–32/1	S to Indo-Malaya	SE United States
Theaceae	*Stewartia*	7–10/2	incl. *Hartia*, S to Indochina	E United States
Umbelliferae	*Glehnia*	1/1	NE Asia	Pacific N. Am.

APPENDIX 1. (Continued).

Family	Genus	Number of Species in E. Asia/ N. Am.	Distribution in E. Asia	Distribution in N. Am.
Umbelliferae	*Osmorrhiza*	1+/10–14	W to Caucasus	S to Andes
Vitaceae	*Ampelopsis*	15/2		
Vitaceae	*Parthenocissus*	9/2		
Alliaceae	*Nothoscordum*	1/2	NE Asia, 4 African	N. Am., 28 S. Am.
Araceae	*Symplocarpus*	2/1	NE Asia	Atlantic N. Am.
Croomiaceae	*Croomia*	2/1		E United States
Cyperaceae	*Trichophorum*	1/3		
Gramineae	*Diarrhena*	1/1		
Gramineae	*Hystrix*	2/3	S to New Zealand	
Gramineae	*Muehlenbergia*	6/94–110		S to Andes
Gramineae	*Schizachne*	1/1		S to Mt. SW United States
Gramineae	*Zizania*	1/1–2	S to Burma	
Liliaceae	*Aletris*	13/5	S to Himalaya	
Liliaceae	*Clintonia*	2/4		
Liliaceae	*Disporum*	8/12	S to Indochina	
Liliaceae	*Smilacina*	14/11	S to Himalaya	Central Am.
Liliaceae	*Zigadenus*	1/20		S to Central Am.
Orchidaceae	*Erythrodes*	3+/97–	S to Indo-Malaya, Polynesia	Argentina
Orchidaceae	*Pogonia*	2/1+		(40 to tropical S. Am.?), S to W. Indies, and tropical S. Am.
Orchidaceae	*Tipularia*	2/1	N to E Asia	
Trilliaceae	*Trillium*	3+/ca. 40	Kamchatka to W Himalaya	
Zosteraceae	*Phyllospadix*	2/3		Pacific coast of N. Am.

APPENDIX 2. Paired genera of Eastern and Western hemispheres.

Family Name	Genus in Eastern Hemisphere (Species number, distribution)	Genus in Western Hemisphere (Species number, distribution)
Cupressaceae	*Calocedrus* (2)	*Heyderia* (1)
Taxodiaceae	*Glyptostrobus* (1)	*Taxodium* (3, to Mexico)
Berberidaceae	*Epimedium* (21, W to Mediterranean)	*Vancouveria* (3, Pacific N. Am.)
Podophyllaceae	*Plagiorhegma* (1)	*Jeffersonia* sensu stricto (1)
Saururaceae	*Houttuynia* (1)	*Anemopsis* (1)
Papaveraceae	*Macleaya* (2)	*Bocconia* (1)
Hydrangeaceae	*Deutzia* (50)	*Neodeutzia* (1–3, Mexico)
Rosaceae	*Rhodotypos* (1)	*Neviusia* (1, SE United States)
Hamamelidaceae	*Distylium* (15, to Malaysia, Java)	*Molinadendron* (3, to Mexico, Central Am.)
Fagaceae	*Castanopsis* (120, to tropics)	*Chrysolepis* (2, W United States)
Cornaceae	*Dendrobenthamia* (12)	*Benthamidia* (*Cynoxylon*) (3, to Central Am.)
Caprifoliaceae	*Weigela* (12)	*Diervilla* (3)
Campanulaceae	*Homocodon* (1, Yunnan)	*Heterocodon* (1, W N. Am.)

TEMPERATE FLORAS: THE NORTH PACIFIC CONNECTION

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ABSTRACT

The affinities between the floras of eastern Asia and eastern North America are widely recognized, but close affinities also exist between some elements of the floras of northeastern Asia (China, eastern USSR, and Japan) and northwestern North America. This relationship is indicated in taxonomic treatments either by no formal taxonomic recognition of the disjunct populations, or by varietal or specific separation of the disjuncts. After listing 31 examples of this disjunction, I offer a protocol for their comparative, evolutionary study. In addition to making careful morphological and cytological comparisons, it should be possible to test the degree of genetic similarity and ecological comparability of the vicariants. By growing them for use in breeding tests, allozyme studies, and for controlled environment testing, it should be possible to determine the degree of genetic similarity or divergence that the vicariants may reveal. By comparing physical and biotic aspects of their ecologies, one could assess their habitat/niche similarities. Data from such studies can test either of two hypotheses: (1) The disjuncts are conservative and have not diverged in any significant way since their separation. (2) The disjuncts have diverged to become passively genetically isolated *and* ecophysiologically distinct, despite their close taxonomic affinity. At present, only very few examples of paired genetic-ecologic tests are known.

Over the years—and at this present symposium—botanists and biogeographers have emphasized the connections between the floras of eastern Asia and those of eastern North America. From Linnaeus, Frederick Pursh, and Asa Gray to contemporary phytogeographers (Graham, 1972; Li, 1952, 1972), the causes and consequences of the floristic connections between the two continents' eastern areas have occupied the geobotanical stage. Yet a few botanists have noted the substantial affinities between temperate eastern Asia and the northwestern Pacific side of North America. Papers by Hara (1952, 1956) and Mizushima (1972) remind us that the North Pacific rim from Japan and mainland China to the American Pacific Northwest provides a large number of floristic links between the oriental Old World and the western New World.

It has been remarked (Mizushima, 1972) that the North Pacific connection has been overlooked probably because the contemporary floras are in the main so different. Through the early to mid Tertiary, a nearly continuous mixed mesophytic forest maintained the floristic similarities between eastern Asia and much of temperate North America. Then, climatic changes, no doubt ushered in by massive orogenies in the Pacific Northwest, largely obliterated the mixed mesophytic forest type in the Pacific Northwest (Graham, 1972).

What affinities remain, though, are substantial and suggest that some taxa survived the erasures of much of that flora of the late Tertiary. Or, perhaps, the Pacific Northwest in the late Tertiary developed floristic elements that spread from east to west—up the coast of western North America and down the east coast of Asia. Could, for example, vicariants in *Lysichitum* and *Rubus* have arrived in eastern Asia in a counter-clockwise migration? Further, it is probable that the number of vicariants and disjunctions in the North Pacific floras might have diminished further during the Pleistocene. So, we have a set of biogeographic conundrums for many plant distributions along the North Pacific rim. Questions that these bicontinental distributions pose to the student of evolution are also genetic ones. How much genetic "distance" separates the vicariants? Have the vicariants become reproductively isolated in the passive, allopatric mode, or are some still inter-fertile?

This paper first reviews some of the examples of the North Pacific floristic connection and then proposes ways to test the degree of genetic divergence between vicariant taxa.

EXAMPLES OF EASTERN ASIA–WESTERN NORTH AMERICA FLORISTIC AFFINITIES

Vascular plants with amphi-Pacific affinities can be categorized in three modes: taxonomic, geographic, and ecological. Furthermore, these

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TABLE 1. Some taxa of eastern Asian–western North American affinities.

Eastern Asia	Western North America	Range	Continuity	Habitat	Taxonomic Status
Woodwardia orientalis Sw.	*W. fimbriata* J. E. Smith	Japan & Washington	Discontin.	Mesic coastal to montane	Vicar. spp.
Cryptogramma crispa (L.) R. Br.	*C. crispa*	Circumboreal	Discontin.?	Mesic-xeric, coastal/montane	Conspecific
Pinus thunbergii Parl.–*P. densiflora* Sieb. & Zucc.	*P. contorta* Loud.	Circumboreal	Discontin.	Mesic-xeric, coastal/montane	Vicar. spp.
Calamagrostis purpurascens R. Br.	*C. purpurascens*	Eastern Asia + western North America	Contin.?	Mesic-xeric, coastal/montane	Conspecific
Deschampsia atropurpurea (Wahl.) Scheele	*D. atropurpurea*	Cosmopolitan	Contin.	Mesic, montane	Conspecific
Lysichitum camtschatcense Schott	*L. americanum* Hultén & St. John	Japan to California	Discontin.	Mesic	Vicar. spp.
Fritillaria camschatcensis Ker	*F. camschatcensis*	Japan to Washington	Contin.?	Mesic, coastal	Conspecific
Maianthemum dilatatum Nels. & MacBr.	*M. dilatatum*	Japan to western North America	Contin.?	Mesic	Conspecific
Platanthera chorisiana Rchb. f.	*P. chorisiana*	Japan to Washington	Contin.	Mesic	Conspecific
Alnus crispa Ait.	*A. crispa* var. *sinuata* Regel	Eastern Asia–western North America	Contin.	Mesic, montane	Vicar. vars.
Coptis japonica Mak.	*C. aspleniifolia* Salisb.	Japan–Southern British Columbia	Discontin.?	Mesic	Vicar. spp.
Achlys triphylla DC. var. *japonica* (Max.) Fukuda	*A. triphylla* var. *triphylla*	Japan to California	Discontin.	Mesic	Vicar. vars.
Saxifraga bronchialis L. ssp. *funstonii* (Small) Hult.	*S. bronchialis* ssp. *austromontana* Pip.	Siberia–North America (circumbor.)	Discontin.	Montane	Vicar. vars.
Geum calthifolium Smith var. *nipponicum* Hara	*G. calthifolium*	Japan to British Columbia	Contin.?	Mesic, coastal	Vicar. vars.
Rubus pedatus J. E. Smith	*R. pedatus*	Japan to southern Oregon	Discontin.?	Mesic-montane	Conspecific
R. vernus Focke	*R. spectabilis* Pursh	Japan to NW California	Discontin.?	Mesic	Vicar. spp.

TABLE 1. (Continued).

Eastern Asia	Western North America	Range	Continuity	Habitat	Taxonomic Status
Spiraea betulifolia Pallas ssp. *aemiliana* Hara	*S. betulifolia* ssp. *lucida* (Dougl.) Hitch.	Circumboreal?	Contin.?	Mesic-xeric	Vicar. spp.
Oplopanax horridum (Smith) Miq. var. *japonicum* Hara	*O. horridum*	Eastern Asia–western & central North America	Discontin.	Mesic	Vicar. vars.
Acer japonicum Thunb.	*A. circinatum* Pursh	Japan–Northern California	Discontin.	Mesic, coastal	Vicar. spp.
Cassiope stelleriana (Pall.) DC.	*C. stelleriana*	Eastern Asia to Washington	Contin.?	Mesic-montane	Conspecific
Menziesia pentandra Maxim.	*M. ferruginea* Smith	Japan–Oregon	Discontin.	Mesic-coastal	Vicar. spp.
Rhododendron kamtschaticum Pall.	*R. kamtschaticum*	Japan to Alaska	Contin.?	Polar/boreal	Conspecific
Fauria crista-galli Makino ssp. *japonicum* Gillett	*F. crista-galli*	Japan to Washington	Contin.?	Mesic-coastal	Vicar. vars.
Boschniakia rossica Fedtsch.	*B. rossica*	Eastern Asia–Alaska	Contin.?	Mesic-coastal	Conspecific
B. rossica	*B. hookeri* Walpers	Eastern Asia–Washington	Contin.?	Mesic-coastal	Vicar. spp.
Galium kamtschaticum Stell. var. *acutifolium* Hara	*G. kamtschaticum* var. *oreganum* Piper (= *G. oreganum*)	Eastern Asia–Oregon	Contin.?	Mesic-coastal	Vicar. vars.
Valeriana sambucifolia Mikan var. *fauriei* Hara	*V. sitchensis* Bong.	Eastern Asia–California	Discontin.	Mesic-montane	Vicar. spp.
Campanula lasiocarpa Cham.	*C. lasiocarpa*	Japan–Washington	Contin.?	Montane	Conspecific
Artemisia arctica Less. ssp. *arctica*	*A. arctica* ssp. *arctica*	Japan–western North America	Contin.?	Boreal/montane	Conspecific
Achillea sibirica Ledeb.	*A. sibirica*	Japan–British Columbia	Contin.?	Montane?	Conspecific
Erigeron thunbergii A. Gray	*E. glaucus* Ker	Japan–California	Discontin.	Coastal	Vicar. spp.

categories are best viewed as elements of overlapping, multidimensional matrices. For example, some are strictly amphi-Pacific plants [*Achlys triphylla* (Smith) DC.] that are conspecific throughout their North Pacific distributions; others are circumboreal [*Cryptogramma crispa* (L.) R. Br.] or circumpolar [*Phippsia algida* (Sol.) R. Br.]. Some taxa are differentiated into varieties/subspecies or species along the North Pacific rim. Others are indistinguishable taxonomically. Some north Pacific taxa reach the full extent of the distributional arc, from Japan or adjacent mainland Asia, more or less continuously to the southern limit of the Pacific Northwest in northern California; others go only part of the way—for example, from Japan to the Aleutians or to Alaska. These are but some of the permutations of the amphi-Pacific floristic theme. Table 1 samples some of the various types of amphi-Pacific continuity.

From Table 1 we can glean some inferences about amphi-Pacific distributions: most examples are herbaceous perennials with coastal, mesic ecologies; bog species are common; and, apart from circumboreal and circumpolar examples, the strictly circum-Pacific cases can range from eastern Asia to western North America more or less continuously while others reach North America discontinuously (only the Aleutians, Alaska, British Columbia, or Washington).

No one can be sure what these variant distribution patterns are trying to tell us. I suspect they are the combined result of obvious phenomena: (1) the capriciousness of dispersal/distribution, (2) specific physiological tolerance ranges, and (3) the influence of past glacial and orogenic events.

Some Geological History in the North Pacific Area

The time from the Paleocene to the present (ca. 75 million years) has spanned major geological and climatic changes. The major phenomena include change in coastlines (including the flux of epiric seas); sea floor spreading; episodes of orogeny, especially vulcanism; and Pleistocene glaciation (and interglacial/post-glacial ameliorations). Through this span of turbulent time, floras waxed and waned, but remnants of floras had to persist to give their present amphi-Pacific distribution.

The early Tertiary seemed to have provided the most continuous stretch of habitat for temperate taxa. The mixed mesophyte forests of those times did pervade the North Pacific land masses (Wolfe, 1969, 1972). And, by the Miocene, most of the major floristic elements of the North Pacific rim were in place. Climatic change and geologic upheaval intervened to disrupt the continuities in varying degrees—from extinctions to major disjunctions. The latest perturbations, the Pleistocene ice encroachments, were the most recent to have affected this fluid, transitory biota.

It is instructive to note that Li (1952) inferred a difference in age among the various vicariants between the New and Old worlds. He (Li, 1952: 373) pointed out that the western North American–eastern Asian group of plants is a different and more recent one than the eastern Asian–eastern North American group. Li bases this assertion on (1) the relatively continuous, rather than discontinuous distribution of the amphi-Pacific plants; (2) their coastal, cool temperate to arctic distribution; and (3) their predominant herbaceous life-form. Li's arguments remind us that the intercontinental migrations and confluences of taxa (and of floras?) have taken place repeatedly throughout the past, have taken different paths, and today are expressed in a range of discontinuities.

Genetic Affinities of Vicariants and Disjuncts

It is assumed that the plants that show eastern Asia–western North America similarities are closely monophyletic (conspecific to vicariant taxa). It then follows that each example should show some degree of genetic affinity. Morphological resemblance is, of course, the initial basis for inferring genetic similarity. Further testing of the inferences of relationship from morphology must rely on genetic methods. Attempts to cross vicariants is a necessary next step. Degree of crossability and interfertility can be valuable measures of affinity. Other tests of genetic affinity could include isozyme comparisons via gel electrophoresis and could eventually employ comparisons of DNAs of paired taxa. For now, we will consider the evidence from crossing tests.

Several alternative hypotheses regarding genetic affinity of amphi-Pacific taxa are testable: (1) vicariants or disjuncts are conservative and have not diverged in any significant way and are interfertile; (2) disjuncts and vicariants have diverged to become genetically incompatible (either low crossability or reduced interfertility) and thus are reproductively isolated. It is to be expected that each particular pair of taxa will validate one

or the other of these hypotheses. Besides genetic/reproductive isolation, another component of potential genetic difference is surely to be ecotypic differentiation of vicariants or disjuncts. From other genecological studies (e.g., Clausen & Hiesey, 1958; Clausen et al., 1940, 1948), one would predict that even conspecific taxa in Asia and western North America will possess detectable ecophysiological differences that are bound to be genetically fixed.

In what follows, I review some of the evidence from crossability studies as it bears on the issue of genetic affinity between bicontinental disjuncts. Not all the examples illustrate the western North American–eastern Asian theme of this paper; rather, they illustrate the more general notion of degrees of genetic relationship between congeneric taxa in different continents. Thus, cases involving pines and certain hardwoods (e.g., *Liriodendron*) relate to connections via the north Atlantic between the Old World and the New, rather than to the North Pacific connection.

Few or no deliberate crosses have been performed to test either reproductive isolation or the ecotypic differentiation hypotheses as they apply to Asian–North American taxa. However, some bits of evidence come to light from horticultural, forestry, and agronomic literature, as follows:

Conifers. Breeding tests by Wright (1955) with *Picea* species from North America and Asia range from successful crossability (*P. jezoensis* × *P. glauca*) to unsuccessful (*P. asperata* × *P. sitchensis*).

Examples from *Pinus* (Mirov, 1967) include the curious case of *P. lambertiana*. It does not hybridize naturally with any of its western North American congeners, yet it is successfully crossed with two eastern Asiatic pines, *P. koraiensis* and *P. armandii*, also of the soft pine (*Haploxylon*) affinity. Intentional crosses among some Diploxylon pines from eastern Asia and western North America have been reported as failures (Duffield, 1952).

Broad-leaved trees. The Palmatum group of maples (*Acer*) is largely Asiatic. The one western North American species, *A. circinatum*, fails to cross with either *A. palmatum* or *A. japonicum*, both of Japan (fide J. A. Witt, University of Washington Arboretum).

Parks et al. (1983), at this symposium, reported that crosses between *Liriodendron tulipifera* (eastern North America) and *L. chinensis* (Hupeh, China) yield viable F_2 seed. Isozyme and flavonoid comparisons, coupled with the crossing data, indicate that the two taxa "... have not diverged very far from a presumed common ancestor ...."

Other woody plants. Crosses within and between series (= sections, more or less) in *Rhododendron* are often successful, yielding progeny of varying fertilities. The well-known azalea hybrids of the Knaphill and Koster origins are crosses of *R. occidentale* (western North America) with eastern Asiatic species, especially *R. japonicum*. Crossability and fertility is mainly high in these crosses with subseries *Luteum*. Asiatic members of series *Ponticum* have been crossed successfully with our western North American, *R. macrophyllum*.

Herbaceous monocots. *Iris* hybridizers have included some eastern Asia–western North America crosses in their many attempts to improve *Iris* for horticulture. Four different types of crosses all have yielded sterile F_1 progeny (fide Jean Witt, Seattle): *Iris* section *Sibiricae* × *I. setosa* (North American), *I. sibirica* × *I.* section *Californicae* (the so-called "*cal-sib*" hybrids), *I. douglasiana* × *I. lactea* (central Asia to Korea), and *I. longipetala* (northern California) × *I. sibirica*.

Herbaceous dicots. Very few cases of intentional crossings between eastern Asian and western North American congeners were found. Given the very rich but diffuse literature on plant breeding, more cases will surely come to light.

Taylor's (1967) study of intentional crosses in *Aquilegia* includes the hybrid *A. flabellata* (Japan) × *A. flavescens* (western North America); the F_1 had 61% stainable pollen and normal meiosis.

The scanty record of intentional hybridization between eastern Asian and western North American taxa makes it fruitless to draw any conclusions. Only when a program of deliberate crossing is mounted, involving a whole range of amphi-Pacific plants, can we test the genetic bases of the "North Pacific Connection." Many of the plants of Table 1 would be ideal subjects for such genetic testing. Indeed, the fuller lists of Mizushima (1972) and Hara (1952, 1956) provide ample taxa for pioneering a genetic analysis of amphi-Pacific biogeographic connections.

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THE FLORISTIC RELATIONSHIPS OF THE TEMPERATE FOREST REGIONS OF CHINA AND THE UNITED STATES[1]

TSÜN-SHEN YING[2]

ABSTRACT

A diagrammatic illustration is used to explain the meridional shift of the constituents of the Chinese deciduous forests from one in Regions I and II with deciduous trees and few evergreen undershrubs to one in Region III with deciduous species forming the canopy and some evergreen undergrowth, and to one in Region IV with deciduous and evergreen trees mixed. Five samples from the temperate forests of Region III, IV, and VIII are selected to explain the altitudinal variation of the Chinese deciduous forests from eastern to western China, with their obvious limit in western Sichuan and the immediately adjacent portion of Yunnan. A list of the paired or closely related species dominant in the forests is provided to demonstrate the affinities of the deciduous forests of China and the United States. The exact nature of the floristic relationship is explained by distributional maps showing (1) disjunction of the species of *Clintonia* Raf. with centers of distribution in China, Japan, western United States and the eastern United States, (2) bicentric pattern of distribution of *Diphylleia* Michaux in eastern Asia and eastern United States, (3) bicentric distribution of *Kelloggia* Torrey ex Bentham & Hooker restricted to China (Yunnan) and the western United States.

SPECIAL FEATURES OF THE TEMPERATE FORESTS OF CHINA

South China is under the influence of a monsoon climate and its characteristic vegetation is one of mesophytic forests. Northwestern China is arid land occupied by steppes and deserts. Consequently, the vegetation of China is recognized as being composed of eight major types, Regions I–VIII (Fig. 1, Wu, 1980). Regions I to III and the northern portion of Region IV support temperate forests.

Based on the composition, structure, and physiognomy of the communities, these forests can be recognized as deciduous broad-leaved forests and coniferous forests. Generally speaking, the climate of the areas supporting deciduous forests is hot and rainy in the summer, and cold and dry in the winter. The mean annual temperature and precipitation for Regions II–IV are shown in Table 1.

There is an obvious meridional shift of the constituents of the increased number of evergreen species replacing the deciduous ones in the temperate forests of China. The composition of different forests is modified in accordance to the location of each community. From north to south, a few low evergreen shrubs enter the deciduous broad-leaved forests of Region II. As hydrothermal conditions gradually increase, evergreen trees enter the temperate forests in the southern areas as the second layer of the communities. As the hydrothermal condition increases continuously southward, evergreen and deciduous broad-leaved species become mixed in the forests. In still more southerly regions evergreen broad-leaved species replace the deciduous ones (Fig. 2).

Another outstanding characteristic of the temperate Chinese forests is the variation from east to west. For example, the deciduous forests of Huangshan in Anhui occur at an elevation of 1,000 to 1,600 m. In Shennongjia in western Hubei, the deciduous forests occur at 1,700 to 2,200 m. On the southern slopes of the Qinling Mountains the deciduous forests occur at 1,800

TABLE 1. Mean annual temperature and precipitation in Vegetation Regions II–IV.

Region	Mean Annual Temperature °C	Mean Annual Precipitation mm
II	0.3–5.5	562.6–657.8
III	7.8–14.3	584.0–835.8
IVB	14.3–15.4	903.9–1,134.4

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FIGURE 1. The vegetation regions of China (simplified from Wu, 1980). I = Cool temperate coniferous forest region; II = Temperate coniferous deciduous broad-leaved mixed forest region; III = Warm temperate deciduous broad-leaved forest region; IV = Subtropical evergreen broad-leaved forest region, IVA = North subtropical evergreen deciduous broad-leaved mixed forest subregion, IVB = South subtropical monsoon evergreen broad-leaved forest subregion; V = Tropical monsoon and rain forest region; VI = Temperate steppe region; VII = Temperate desert region; VIII = Qinghai-Xizang plateau vegetation region.

to 2,600 m (Chiu & Chin, 1957; Chow, 1965; Ying et al., 1979). The deciduous broad-leaved forests disappear in western Sichuan and northwestern Yunnan Provinces (Fig. 3).

Complexity is another feature of the Chinese deciduous forests. Approximately 930 genera are recognized in the temperate forests of China (Wu, 1965). Owing to geographic transformations and changing combinations of environmental factors throughout geological time, these genera have achieved different distributional patterns. They have been classified into the following types: (1)

FIGURE 2. The gradual meridional change of constituents of the deciduous forests in China.

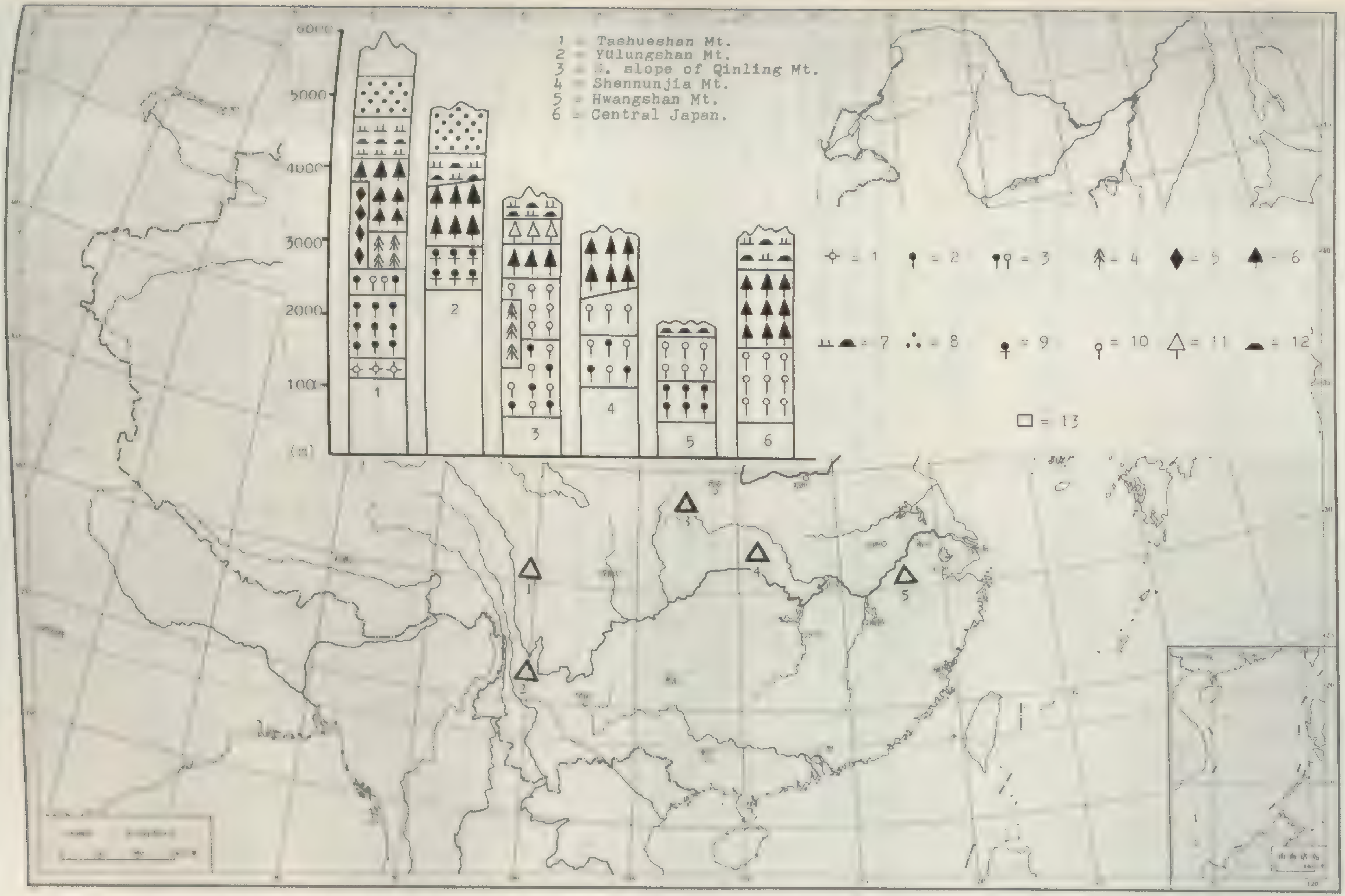

FIGURE 3. Altitudinal change of deciduous forests from east to west in eastern Asia. 1 = Succulent thorny scrub; 2 = Evergreen broad-leaved forest; 3 = Evergreen deciduous broad-leaved mixed forest; 4 = Temperate coniferous forest; 5 = Sclerophyllous evergreen broad-leaved forest; 6 = Evergreen coniferous forest; 7 = Alpine meadow and bush-wood; 8 = Subniveal open vegetation; 9 = Pine forest; 10 = Deciduous broad-leaved forest; 11 = Deciduous coniferous forest; 12 = Subalpine scrub.

TABLE 2. Eastern Asian endemic families represented in the deciduous forests of China and adjacent floristic regions.

Family	Total Number of Genera/Species	Genera/Species in China	Range
Ginkgoaceae	1/1	1/1	China–Japan?
Cephalotaxaceae	1/9	1/7	China–Japan
Nandinaceae	1/1	1/1	China–Japan?
Cercidiphyllaceae	1/1	1/1	China–Japan
Trapellaceae	1/2	1/1	China–Japan
Sargentodoxaceae	1/1	1/1	China only
Eucommiaceae	1/1	1/1	China only
Davidiaceae	1/1	1/1	China only
Tetracentraceae	1/1	1/1	Sino–Himalayan
Toricelliaceae	1/3	1/2	Sino-Himalayan
Eupteleaceae	1/2	1/1	Sino-Himalayan–Japan
Helwingiaceae	1/4	1/4	Sino-Himalayan–Japan

North Temperate Zone genera (ca. 300); (2) eastern Asian genera (298); (3) temperate Old World genera (157); (4) temperate Asian genera (63); (5) eastern Asian–North American genera (115). Of these, the North Temperate Zone genera, eastern Asian genera, and eastern Asian–North American genera are more prominent in the composition of the temperate forests of China. Genera such as *Acer, Carpinus, Populus, Salix, Fagus, Castanea, Prunus, Sorbus,* and *Tilia* are found in the temperate forests throughout the northern hemisphere. The greatest concentration of species in some of these genera is in China, especially in central China. For example, the genus *Acer* contains about 200 species worldwide. Almost three-fourths of the species occur in China, distributed south of the Qinling Range and east of southeastern Tibet, and 42 species are concentrated in central China (eastern Sichuan and western Hubei). *Dipteronia,* the only other genus of the Aceraceae, is almost totally restricted to this same region. Another genus with similar species concentration is *Carpinus,* with 40 species worldwide, of which 25 are restricted to central and southwestern China.

Antiquity is another feature of the Chinese deciduous forests. For example, *Carpinus hupehana,* distributed in central China, is morphologically close to the fossil species *C. miofargesiana* (Tanai, 1972). Fossil species of *Carpinus* are also found in Tertiary deposits of North America and Europe. The occurrence of extinct and extant species of a genus in the same area is an indication of the antiquity of the community in which the living species occurs.

High endemism is another prominent feature of the Chinese deciduous forests. At the family level there are many monotypic or oligotypic, endemic families. Table 2 shows that there are 12 families with distributions limited to China and adjacent floristic regions. Two of these families are gymnosperms. The Ginkgoaceae, represented by *Ginkgo biloba* L., a "living fossil," existed during the Triassic Period. Another gymnosperm family, the Cephalotaxaceae, is represented by a single genus, *Cephalotaxus,* with nine species, of which seven occur in China, especially in central China. Of the ten families of angiosperms, Eupteleaceae, Tetracentraceae, Toricelliaceae, and Helwingiaceae (the latter two often placed in the Cornaceae) are of Sino-Himalayan or Sino-Japan-Himalayan distribution. Cercidiphyllaceae is represented by two varieties of a monotypic genus occurring disjunctly in central China and Japan. Davidiaceae (also sometimes placed in the Cornaceae) and Sargentodoxaceae are endemic to China. Some of these families have fossil records in North America and Europe in Neogene or older strata.

Floristic Relationship Manifested Through the Deciduous Forests of China and the United States

Broad-leaved deciduous forests prevail in the north temperate zone and are particularly well developed in China, Japan, the eastern United States, Europe, and the Caucasus Mountains (Daubenmire, 1978; Numata, 1974; Wu, 1980). The similarities of the geographical characters.

TABLE 3. Comparison of the composition (trees) of the temperate deciduous forests in eastern North America and China. Not arranged according to dominance or closeness of relationship. (Derived in part from field work in China and the United States and from Fernald, 1950; Jepson, 1925; and Seymour, 1969.)

China	Eastern North America
Acer buergereianum	*Acer rubrum*
A. mono	*A. saccharum*
Alnus japonica	*Alnus maritima*
A. nepalensis	*A. serrulata*
Aesculus chinensis	*Aesculus octandra*
Betula albo-sinensis	*Betula alleghaniensis*
B. chinensis	*B. lenta*
B. dahurica	*B. nigra*
B. platyphylla	*B. populifolia*
Carpinus turczaninowii	*Carpinus caroliniana*
	Carya cordiformis
	C. glabra
	C. tomentosa
Chosenia arbutifolia	
Cornus chinensis	*Cornus florida*
Cornus macrophylla	
Fagus longipetiolata	*Fagus grandifolia*
F. lucida	
Fraxinus mandshurica	*Fraxinus americana*
Halesia macregorii	*Halesia monticola*
Juglans mandshurica	*Juglans cinerea*
J. cathayensis	*J. nigra*
Liriodendron chinense	*Liriodendron tulipifera*
Magnolia officinalis	*Magnolia acuminata*
	M. fraseri
	M. macrophylla
	M. tripetala
Malus baccata	*Malus angustifolia*
M. sieversii	
Quercus acutissima	*Quercus alba*
Q. aliena	*Q. coccinea*
Q. aliena	*Q. falcata*
var. *acutiserrata*	*Q. laevis*
Q. dentata	*Q. laurifolia*
Q. liaotungensis	*Q. prinus*
Q. mongolica	*Q. rubra*
Q. variabilis	*Q. velutina*
Tilia amurensis	*Tilia americana*
T. chinensis	*T. heterophylla*
Ulmus propinqua	*Ulmus americana*
U. pumila	*U. rubra*

climatic conditions, and vegetation composition of the deciduous forests of China and the eastern United States are closer than those between China and Europe and the Caucasus. This phenomenon has attracted the interest of numerous phytogeographers. The dominant species of the deciduous forests of China and the eastern United States are often paired or closely related taxa of the same genera, as shown in Table 3.

TABLE 4. Some common shrubs and herbs in Chinese and American temperate deciduous forests. Arrangement does not necessarily indicate close relationship. (Derived in part from Fernald, 1950; Jepson, 1925; and Seymour, 1969.)

China	United States
Adiantum pedatum	*Adiantum pedatum*
Clintonia udensis	*Clintonia umbellulata*
Convallaria keiskei	*Convallaria montana*
Hydrangea umbellata	*Hydrangea arborescens*
	Kalmia latifolia
Maianthemum bifolium	*Maianthemum canadense*
Pyrola rotundifolia	*Pyrola rotundifolia* var. *americana*
Rhododendron micranthum	*Rhododendron maximum*
Ribes meyeri	*Ribes cynosbatii*
Tiarella polyphylla	*Tiarella cordifolia*
Trientalis europaea	*Trientalis borealis*
Vaccinium japonicum	*Vaccinium erythrocarpum*
V. uliginosum	*V. constablaei*
	V. vacillans

The relationship is not limited to the dominant tree species. The understory shrub layer and the herbaceous species of the deciduous forests also contain many genera common to the two regions, as shown in Table 4.

In the temperate floras of China and the United States there are about 115 genera with disjunct distribution. Approximately 50 of these are oligotypic genera. In order to explain the floristic relationship between Asia and North America, the following genera restricted to China and/or Japan and eastern North America are selected: *Cornus* section *Thelycrania* (1:1); *Chionanthus* sensu stricto (1:1); *Caulophyllum* (1:1); *Decumaria* (1:1); *Diphylleia* (2:1); *Halesia* (1:3); *Hamamelis* (2:4); *Jeffersonia* (1:1); *Liriodendron* (1:1); *Menispermum* (1:1); *Mitchella* (1:1); *Sassafras* (1:1); *Stylophorum* (1:1); and *Kelloggia* (1:1). The figures in parentheses are the numbers of species in each area, eastern Asia to the left, eastern North America to the right.

The above species manifest some of the common characteristics of the flora of eastern Asia and eastern North America. These can be divided into three different distributional patterns: 1) eastern Asian–eastern North American (Fig. 4);

FIGURE 4. Bicentric distribution of *Diphylleia* in eastern Asia and eastern North America.

2) eastern Asian–western North American (Fig. 5); and 3) eastern Asian–eastern and western North American (Fig. 6).

In addition, the monotypic or oligotypic families such as Schisandraceae, Iteaceae, Saururaceae, and Illiciaceae are of special interest. In the deciduous genus *Schisandra*, the primitive section *Pleiostema* and the advanced section *Sphaerostema* both have a disjunct pattern of distribution from China southward to Sumatra and Java (Smith, 1947). Only one species, *Schisandra glabra*, belonging to section *Schisandra* is known in eastern North America; two species of this section are in eastern Asia (Smith, 1947). Likewise, in the genus *Itea*, most species occur in eastern Asia and thence southward to Java. Again, there is only one species in southeastern North America. The family Saururaceae contains seven species in three genera scattered in eastern Asia and North America. The genera *Houttuynia* and *Anemopsis* and the counterpart species *Saururus chinensis* and *S. cernuus* occur in the two widely separated regions. The genus *Houttuynia* is distributed in eastern Asia and

FIGURE 5. Bicentric distribution of *Kelloggia* in eastern Asia and western North America.

FIGURE 6. Tricentric distribution of *Clintonia* in eastern Asia and eastern and western America.

southward to Indonesia. The genus *Saururus* occurs in Vietnam. The genera restricted to North America and eastern Asia not only indicate a close floristic relationship between the two regions, they also provide reliable clues to their tropical origin.

Almost all of the plants mentioned above grow in temperate deciduous forests in both regions. Detailed studies, including morphology, coupled with ecology, plant sociology, and cytology, will provide many clues that will be of great importance in understanding the patterns of disjunction in plant distribution.

CONCLUSIONS

The deciduous forests of China represent a complex old flora. The dominant species belong to genera having a Tertiary history. There is an evident gradual meridional shift of the constituents from more evergreen species in the south to deciduous ones in the north. The areas occupied by deciduous forests in China were converted to farmland a thousand or more years ago. Remnants of the original forests in steep mountainous regions of Huanshan, Shennongjia, Qinling, Yulungshan, and Tashueshan indicate an altitudinal variation from east to west, accompanied by changes in composition.

Many of the genera have a widespread distribution in the temperate northern hemisphere. A large number of them are common to the deciduous forests of China and the United States. The shared genera include the dominant trees, shrubs and herbaceous plants. Many of these shared plants are not limited to large genera with widespread distribution but often belong to small, oligotypic genera such as *Liriodendron* and *Sassafras*.

The nature of the floristic relationship between the deciduous forests of China and the United States is exhibited by a tricentric distributional pattern in such genera as *Clintonia* with species in China, Japan, western United States, and eastern United States, a bicentric distributional pattern as in *Diphylleia* with species in China, Japan, and the southeastern United States, and another pattern of bicentric distribution in genera such as *Kelloggia* with species in China and western North America.

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NORTH AMERICAN TREES WITH RELATIONSHIPS IN EASTERN ASIA

ELBERT L. LITTLE, JR.[1]

ABSTRACT

Much information on distribution and taxonomy of North American trees with relationships in eastern Asia, including atlases and monographs, is now available. Eastern Asia is the world's largest and richest source of temperate deciduous hardwoods. Because of splitting of genera and species, relationships are becoming obscured and are primarily generic. Eastern Asia is the geographic region or center with greatest display of remnants of the widespread Arcto-Tertiary flora, while Eastern North America is second, with roughly one-half as many tree species. Europe and Western North America have smaller numbers, perhaps one-fourth. Many tree genera are widespread in all four regions. Most of the possible patterns of distribution are represented. Eastern North America and Eastern Asia have the most tree genera, about 16 in common. The relationships have been overemphasized. They are readily explained by mountain-building and changes in climate, especially Pleistocene glaciation.

A review of temperate North American trees with relatives in Eastern Asia is timely. Much information on distribution and taxonomy, including atlases and monographs, is now available and because of expanded markets for hardwoods there is increased interest in foreign trees for introduction in forestry as well as in horticulture. Also, the relationships among tree genera in North America and eastern Asia are becoming obscured, because of splitting of genera and species. The main conclusions are that these relationships have been overemphasized and are readily explained by earth changes accepted within recent years.

Trees, though an artificial group of large woody plants, are excellent examples for biogeographical studies. They are large, conspicuous, relatively well known, of moderate numbers of species, and of economic importance. Thus, their classification has been studied in detail, and their geographic distribution has been mapped. Also, they are preserved as fossils and have a historical record, though with many gaps.

Review of literature. Certain similarities in the floras of temperate Eastern North America and Eastern Asia have long attracted the attention of botanists. These observations have been traced back to Carolus Linnaeus in 1750, Carl Pehr Thunberg in 1784, Luigi Castiglioni in 1790, and Asa Gray (Graham, 1972). Asa Gray (1840, 1846, 1859, 1873, 1878) made important contributions, some reprinted by Sargent (1889), Graham (1972), and Stuckey (1978). The notes made by Gray in 1840 were in a book review written when he was only thirty years old. As early as 1859, Gray cited the work of Darwin and Wallace on natural selection and he stressed the effect of glaciation on present distribution. Li (1952, 1972), who knew both regions, made a detailed analysis and reviewed the extensive literature. He prepared worldwide maps showing outline ranges of many tree genera.

Atlases. Accurate distribution maps of most north temperate tree species have been published, replacing the general outlines by Schmucker (1942). No new maps are presented here. Worldwide generic maps have been compiled, especially by Li (1952) and by Meusel et al. (1965–78). Atlas of United States Trees (Little, 1971–81) in six volumes maps approximately 684 tree species native in continental United States including Alaska. The Forest Service Checklist of United States Trees (Little, 1979) further compiles for each of the 216 native genera the worldwide totals of species and their geographic extent, and cites authors of scientific names, omitted here. Native Trees of Canada (Hosie, 1979) similarly describes, illustrates, and maps the species of that country.

For Europe there are detailed maps of vascular plants of the northwestern part (Hultén, 1950), central region (Meusel et al., 1965–78), and the continent (Jalas & Suominen, 1972–80, incomplete).

Two volumes of an atlas of the trees and shrubs of the Soviet Union have appeared (Bot. Inst.

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Komarova, 1977). Maps for southwest Asia, or Asia Minor, are being published with financial assistance from the United States Public Law 480 program (Browicz, 1978). For Japan there are similar atlases of forest trees (Japan Forest Technical Association, 1964–71) and the flora (Hara, 1958–59; Horikawa, 1972–76).

Monographs. Additional information on distribution with species maps is available in current worldwide taxonomic monographs of north temperate tree genera. Examples are: *Abies* (Liu, 1971; supported by Public Law 480); *Aesculus* (Hardin, 1957, 1960); *Alnus* (Murai, 1964; Furlow, 1979); *Catalpa* (Paclt, 1952); *Cupressus* (Silba, 1981; Wolf & Wagener, 1948); *Illicium* (Smith, 1947); *Lyonia* (Judd, 1981); *Nyssa* (Eyde, 1966); *Osmanthus* (Green, 1958); *Pinus* (Mirov, 1967); *Sassafras* (Keng, 1953); and *Stewartia* (Spongberg, 1974). For *Pinus*, subdivisions as well as species have been charted (Critchfield & Little, 1966; Little & Critchfield, 1969). Other generic monographs cover geographic regions, such as North America.

Forestry. Deciduous hardwoods (dicotyledons) are important in forestry as well as horticulture. The Society of American Foresters at its annual meeting on Sept. 20–22, 1982 at Cincinnati, Ohio, stressed the main subject or theme: "America's Hardwood Forests—Opportunities Unlimited." Seeds and other germplasm are desired for tree breeding or genetics research programs. Eastern Asia is the world's largest and richest source of temperate deciduous hardwoods. Thus, many related species are available for introduction, selection, and hybridization. Also, Old World genera merit testing in new environments, hopefully pest-free, in the New World. Foresters are actively exchanging seeds, information, and expertise.

Relationships. Li (1952) observed that the floristic relationships are primarily generic and not specific. Recent work (such as that cited above) has resulted in the recognition of distinct species in the two geographical areas.

Tree Species in Both Temperate North America and Eurasia

Many species pairs of morphologically similar and apparently closely related tree species have been listed from Eastern North America and Eastern Asia. Li (1972) included examples from these tree genera: *Acer, Aralia, Cornus, Diospyros, Ilex, Rhus, Styrax,* and *Symplocos.*

At present only about five tree species of temperate North America are accepted as native also in Eurasia. Trees are conspicuously absent in long lists of plants on both sides of the North Atlantic Ocean (Hultén, 1958), lists of circumpolar plants (Hultén, 1971), and a list of plants in both Western North America and Japan (Mizushima, 1972). (However, several tropical species, especially mangroves and other beach plants of southern Florida, are common both to New and Old Worlds.)

Juniperus communis, common juniper, perhaps the tree species with greatest range in the world, is circumboreal or circumpolar, extending northward beyond the limit of trees. However, in the New World it is usually a low mat-forming shrub, rarely a small tree.

Two tree species of *Alnus,* alder, are widely distributed, though agreement on classification is lacking. *Alnus incana* of Eurasia has two New World varieties or closely related species: *A. rugosa* in northeastern North America and *A. tenuifolia* in northwestern North America. *Alnus sinuata,* often included in the shrubby species *A. crispa,* ranges from northwestern America into northeastern Asia. Also, two tree species of *Salix,* willow, *S. alaxensis* and *S. bebbiana,* extend from northwestern North America into northeastern Asia.

In the past, several other temperate North American tree species or their varieties have been recorded also from eastern Asia. Examples are *Acer rubrum, Alnus maritima, Cephalanthus occidentalis, Fraxinus nigra,* and *Ilex montana.* A few other paired species of *Ilex* are very closely related. *Styrax officinalis,* a tree species of the Mediterranean region, is represented in California by two shrub varieties, var. *californicus* and var. *fulvescens* and in western Mexico by var. *jaliscanus.*

Paleobotanical Evidence

Of course, the study of plant relationships must be based primarily upon the evidence of fossils. A new paleobotany text begins with this sentence: "The only method by which a history of the plant kingdom can be reconstructed is by a study of fossil plants found in the rocks of the earth" (Taylor, 1981: 1).

Paleobotanists are doing a fine job with the mostly incomplete specimens and disconnected scraps now available, though misidentifications have occurred. The work is slow, and the gaps seem almost insurmountable. Meanwhile, per-

haps others may be permitted to consider and evaluate additional lines of evidence for relationships and even to speculate. Unfortunately, some wild speculations have resulted, and the term "hysterical" plant geography has been proposed!

Briefly, the fossil record reveals a widespread occurrence of many modern genera of woody plants, designated as the Arcto-Tertiary flora, more or less uniform across the temperate lands of the Northern Hemisphere, from the close of the Cretaceous period through the Cenozoic Era, roughly 65 million years in duration. Many genera can be traced back that far, though their origins are obscure and the ancestries uncertain.

Western North America has a fossil plant record known in much greater detail than has Eastern North America. For example, Wolfe (1969) in a vegetational history of the Pacific Northwest recorded from the early and middle Miocene flora these 17 tree genera now absent but persisting in Eastern North America: *Carya, Castanea, Catalpa, Cladrastis, Clethra, Diospyros, Fagus, Gordonia, Gymnocladus, Halesia, Ilex, Liquidambar, Liriodendron, Magnolia, Nyssa, Sassafras,* and *Tilia.* Also, these genera now extinct in the New World: *Ailanthus, Cercidiphyllum,* and *Zelkova.*

About the middle of the Miocene epoch, some 15 million years ago, the climate became cooler and the components of the uniform Arcto-Tertiary forest began to migrate, with subsequent disassociations and extinctions occurring. At present, boreal temperate forests extend through land masses across northern North America and Eurasia. Their composition can be described in a very simplified way as follows: southward the forests separate into four main isolated forest regions or centers. Three regions now have the climate of deciduous hardwood forests with a long warm moist growing season and moist soil throughout the year. The fourth, Western North America, has other climatic patterns, such as dry summers, adapted to conifers. Eastern Asia is the geographic region or center with greatest display of the widespread Arcto-Tertiary flora, while Eastern North America is second, with roughly one-half as many tree species. Europe and Western North America have smaller numbers, perhaps one-fourth as many.

The presence and persistence of the Arcto-Tertiary flora and differences in present numbers of tree species in these regions are readily explained by movements of continental land masses unsuspected a century ago and by the continuation of a favorable climate in these regions. Pleistocene glaciation caused regional climatic changes that greatly influenced the distribution of these tree species. The deciduous forests of eastern Asia merged southward into evergreen tropical forests and apparently shifted downward with advances of continental ice sheets and lower temperatures. In eastern North America similar movements of forest zones southward have been documented by pollen analyses or palynology (Davis, 1969). However, the evergreen tropical forest is not continuous southward but is present in the West Indies and on mountains of Mexico and Central America. In southern Europe, the Alps and east-west mountain chains, as well as the Mediterranean Sea, served as barriers to the southward migration before glacial advances. Obviously, extinction of many tree species followed. In Western North America the climates following mountain-building were drier and unfavorable for survival of deciduous hardwoods except a few relicts (*Acer, Alnus*) in moist sites, such as valleys.

Patterns of Distribution

Four northern temperate forest regions can be designated by letter, from west to east (a fifth, the Colchic, from southeastern Europe to Iran, is not considered here): A, Western North America; B, Eastern North America; C, Europe; and D, Eastern Asia. There are 15 mathematically possible combinations: widespread in all four (ABCD), in three regions (ABC, ABD, ACD, BCD), in two regions (AB, AC, AD, BC, BD, CD), and endemic to one region (A, B, C, D). Three combinations, CD, C, and D, are exclusively Old World and omitted here. Three others, AB, A, and B, are New World endemics to be treated separately.

Many tree genera, some with numerous species common and dominant in temperate forests are widespread in all four regions or also beyond and have persisted in different climates (ABCD). Familiar examples, not considered further here, with reference by number to published generic maps by Meusel et al. (1965–78), are: *Abies* (map 20a), *Acer* (map 276b), *Alnus, Betula, Cornus, Crataegus, Fraxinus* (map 340b), *Juniperus* (map 22d), *Larix* (map 21a), *Picea* (map 20c), *Pinus* (map 21c), *Populus* (map 112b), *Prunus* (map 226c), *Quercus* (map 121c), *Salix* (map 112b), and *Sorbus.* A few others, such as *Aesculus, Cercis, Ostrya, Staphylea* (map 275d), and *Taxus*

TABLE 1. Tree genera (7) confined to Eastern North America (United States or also southeastern Canada) and Eastern Asia, with approximate numbers of species (BD). Maps by Li (1952) are cited by number.

Genus	World Total	Eastern North America	Eastern Asia
Chionanthus[a] (map 42)	3	2	1
Cladrastis (map 26)	4	1	3
Gymnocladus (map 25)	4	1	3
Halesia (map 41)	4	3	1
Liriodendron (map 12)	2	1	1
Sassafras (map 16)	3	1	2
Stewartia (map 31)	10	2	8
Totals	30	11	19

[a] The related genus *Linociera*, if united, would add 80–100 species, mostly tropical and subtropical, and cause removal from the list.

(map 19d), have mostly restricted occurrence in the four regions with partly relict species.

The eight remaining combinations involve one or both North American regions with one or both Old World regions. Tree genera under different patterns, with approximate numbers of species, are presented in Tables 1–5. The well-known pattern of Eastern North America and Eastern Asia (BD) is represented by the most tree genera, about 15 (Tables 1 and 2). This group can be divided into two, one extending beyond southward into subtropical regions, such as West Indies and mountains of Mexico and Central America and in southeastern Asia to Indonesia. Pattern BCD has eight genera (Table 3), ABD has five (Table 4), and AD has four (Table 5). Patterns ACD and AC apparently have a single tree genus each, while ABC and BC have none.

Cupressus, cypress, apparently is the only tree genus absent from Eastern North America (ACD) but present in the other three regions. There are eight species in Western North America, including one from Mexico to Honduras, one in the Mediterranean region, and six in eastern Asia, mainly China.

Arbutus, madrone, is limited to two warm temperate regions, Western North America and Europe (AC; map 329c). There are eight or fewer species in Western North America south to Mexico (one to Nicaragua) and about ten others in the Mediterranean region of Southern Europe and Western Asia.

Table 1 summarizes tree genera confined to Eastern North America (United States or also southeastern Canada) and eastern Asia (BD). All seven genera of mostly deciduous hardwoods are small with relatively few species. Cain (1943) observed that these ancient groups were well displayed as relicts in coves, or rich moist valleys of the Southern Appalachians. Li (1952) noted also two paired genera: *Taxodium* with three (or two) species in Eastern North America (one south to Guatemala) and *Glyptostrobus* with one in China; and *Elliottia* with one species very rare and local in Georgia and *Tripetaleia* with two shrub species in Japan (map 36).

TABLE 2. Tree genera (9) confined to Eastern North America and also south to mountains of Mexico, Central America, or West Indies and to Eastern Asia, with approximate numbers of species, including a few shrubs (BD+). Maps by Li (1952) are cited by number.

Genus	World Total	Eastern North America	Mexico, Central America (additional)	West Indies	Eastern Asia
Carya (map 2)	16	11	1		4
Catalpa (map 46)	11	2		5	4
Gordonia (map 32)	31	1			30
Hamamelis (map 23)	6	2	1		3
Illicium (map 14)	42	2	1	2	37
Lyonia (map 32)	35	5	1	24	5
Magnolia (map 13)	76	8	10[a]	8	50
Nyssa (map 35)	5	3			2
Osmanthus	32	1	1		30
Totals	254	35	15	39	165

[a] To Ecuador in northern South America.

TABLE 3. Tree genera (8) of Eastern North America and in both Europe and Eastern Asia but now absent from western North America, with approximate numbers of species (BCD). Maps by Meusel et al. (1965–78) are cited by number.

Genus	World Total	Eastern North America	Europe	Eastern Asia
Carpinus (map 117d)	28	1	2	25
Castanea (map 121b)	12	4	1	7
Cotinus (map 273d)	4	1	1	2
Fagus (maps 120c, 121a)	10	1	2	7
Liquidambar	3	1	(1)[a]	1
Pistacia (map 274a)	10	2[b]	3	5
Tilia (map 280c)	29	4	5	20
Ulmus	46	11[c]	5	30
Totals	142	25	20	97

[a] Southwestern Asia.
[b] One in southern Texas and northeastern Mexico and one in Mexico and Guatemala.
[c] Includes five species in Mexico, one also to Panama.

Table 2 has nine genera of mostly deciduous hardwoods of slightly broader distribution in the same regions (BD+). These genera are mainly small and in the Old World, though *Carya* is better represented in the New World. From Eastern North America one or more species range southward in tropical mountains to Mexico or Central America and/or West Indies. *Magnolia* reaches Ecuador. Distribution in Eastern Asia is greater, projecting southward into tropical mountains to Indonesia.

Table 3 has eight genera mostly widespread across the deciduous forests of the Northern Hemisphere (BCD). They are now absent from Western North America, which currently lacks a deciduous forest climate but were present there in the Miocene. Some species extend slightly southward, such as to Mexico or Panama or to northern Africa or southwest Asia. Largest numbers of species are in Asia. *Buxus* (Meusel et al., 1965–78, map 273b) might be added, with New World species in the West Indies, Mexico, and Central America, though absent northward.

Table 4 has five small genera absent from Europe (ABD). The four genera of conifers were named from Eastern North America and afterwards found in the other regions and were present in Western Europe in the Miocene and Pliocene.

Table 5 has only four genera, which are confined to the arc around the North Pacific Ocean and which may not have been widely distributed in the past (AD). Three genera are mostly broadleaved evergreens of subtropical and tropical

TABLE 4. Tree genera (5) of both Western and Eastern North America and Eastern Asia but absent from Europe, with approximate numbers of species (ABD).

Genus	World Total	Western North America	Eastern North America	Eastern Asia
Chamaecyparis	6	2	1	3
Thuja	6	1	1	4
Torreya	6	1	1	4
Toxicodendron[a]	16	1	5[a]	10
Tsuga	14	2	2	10
Totals	48	7	10	31

[a] Includes shrubs and woody vines and one tree species from Mexico to Brazil.

TABLE 5. Tree genera (4) confined to Western North America and Eastern Asia with approximate numbers of species (AD). Maps by Meusel et al. (1965–78) are cited by number.

Genus	World Total	Western North America	Eastern Asia
Castanopsis[a] (map 121b)	102	2	100
Lithocarpus (map 121b)	101	1	100
Photinia[b]	61	1	60
Pseudotsuga	6	2	4
Totals	270	6	264

[a] Includes one tree and one shrub species in North America also placed in the segregate genus *Chrysolepis*.
[b] The one species in North America also placed in the segregate genus *Heteromeles*.

range in Eastern Asia with a single tree species disjunct in Western North America. Minor differences have been noted. Thus, the segregate genus *Chrysolepis* Hjelmqvist (1948) has been proposed for the two New World species of *Castanopsis*. The segregate genus *Heteromeles* M. J. Roem. (1847) is now generally adopted for the single New World species also united under *Photinia*. *Calocedrus*, if accepted as a segregate from *Libocedrus* (about ten species), would be added to Table 5, with one New World species and two Old World. Genera of deciduous trees are absent.

Endemic Tree Genera

About 23 additional tree genera (discussed below) are now endemic to temperate North America (Little, 1979: 16–19). Some are old and relicts of wider fossil occurrence also in Eurasia, while others may be young. Several others of southern and southwestern United States not mentioned here are subtropical or tropical in origin.

About eight genera that include at least one tree species have natural ranges confined to western North America (A), most with only one or two species, and centering in California, part coastal and subtropical. They are: *Adenostoma*, two species, also in Baja California, Mexico; *Cercocarpus*, six species, about four additional in Mexico; *Fremontodendron*, two species, also in Baja California; *Heteromeles*, one species, often united under *Photinia*, also in Baja California; *Lyonothamnus*, one species, confined to four California islands; *Oemleria* (*Osmaronia*), one species, north to British Columbia; *Sequoia*, one species; and *Sequoiadendron*, one species, segregated from *Sequoia* in 1939.

About 11 genera that include at least one tree species have natural ranges limited to temperate eastern North America (B; Little, 1980). Most are restricted to the United States and have only one species. They are: *Asimina*, eight species, one species extends north to extreme southern Canada; *Cliftonia*; *Elliottia* (the closely related genus *Tripetaleia* with two species in Japan); *Franklinia* (extinct except in cultivation); *Leitneria*; *Maclura*; *Nemopanthus*; *Oxydendrum*; *Pinckneya*; *Planera*; and *Taxodium* (which was widespread in the Arcto-Tertiary province from the Cretaceous on into the Pliocene), two species, one south to Guatemala.

Leitneria with one relict species is in the distinct family Leitneriaceae. Tertiary fossils from Mississippi, Oregon, and western Siberia have been referred here. *Maclura* would not be endemic, if the related genus *Chlorophora* of tropical America and Africa or an Asian genus were united.

Three tree genera have broad natural ranges in temperate North America, both eastern and western (AB) and south into Mexico. *Garrya*, often placed in a separate family Garryaceae, has 14 species of shrubs and trees, mostly in western United States and Mexico, including one south to Panama, also one in the Greater Antilles (Dahling, 1978). This genus with a fossil record back to Miocene apparently originated in the Southwest. *Ptelea* has three species, one in Mexico only (Bailey, 1962), and is recorded back to Eocene in western and eastern states and to Oligocene in Europe. *Robinia* has about ten species including shrubs, mostly eastern, one in Mexico only. Fossils have been referred to this genus in North America and Europe back to Paleocene and in Japan to Miocene.

Young genera. Two endemic tree genera, one western and one eastern, apparently are young and lack a fossil record. *Oemleria* (*Osmaronia*) with one species may have originated from *Prunus*, a genus with about 33 species of trees and shrubs native across North America and 200–400 worldwide. *Oemleria cerasiformis* is a shrub or rarely small tree occurring in mountain canyons from California north to British Columbia. *Oemleria* differs from *Prunus* in having usually five pistils instead of one, flowers unisexual as well as bisexual, and leaf margins entire rather than serrate.

Nemopanthus may have evolved from *Ilex*. The latter has about 15 species in Eastern North America, is extinct in the western part, and is widespread with 300–350 species mostly tropical (Meusel et al., 1965–78, map 274). *Nemopanthus mucronatus* is a shrub or rarely small tree of northeastern United States and southeastern Canada, along and mostly north of the range of *Ilex* in the glaciated region. The relatively new glaciated land and the habitat of wet soil of bogs and swamps would aid a new, pioneer species. *Nemopanthus* differs from *Ilex* in slight flower characters: petals distinct instead of united at base, stamens free and distinct rather than inserted on corolla, and calyx-lobes none or minute. A second species transferred from *Ilex* is controversial, as are three Old World fossils placed here more than a century ago.

Will it be possible to observe the origin of the next new genus of North American trees? One

species of *Abies* local in the Santa Lucia Mountains of Central California merits watching. H. L. Mason in a paper at a scientific meeting in 1957, predicted that this species would be named a new genus. This distinct species at the border of the generic range is so different from all the other 38 species of *Abies* worldwide that it has been placed alone in a second subgenus, *Pseudotorreya.* Interestingly, it has been classed also as the most primitive species (Liu, 1971).

Subdivisions of Genera

Studies of relationships between tree genera of these four separate regions commonly do not extend to the subdivisions, perhaps partly because of difficulties in classification of fossils. However, living or recent species show various patterns of distribution. A good example is the genus *Pinus,* pine, which has about 95 species of wide range in north temperate regions and southward in tropical mountains. It has a fossil record back to early Cretaceous and Jurassic periods (Mirov, 1967: 106). Also, its subdivisions as well as species have been mapped (Critchfield & Little, 1966; Little & Critchfield, 1969). The two main subgenera, *Strobus* or soft pines and *Pinus* or hard pines, are widespread, and their four sections also in both Old and New Worlds. However, the 15 subsections are more restricted, only three in both but four Old World and eight New World. These 15 subsections may be grouped as designated above by letters as: ABCD, 1 subsection; ACD, 1; BCD, 1; AB, 1; A, 6; B, 1; CD, 1; C, 1; D, 2.

The genus *Pinus* apparently originated in temperate Eastern Asia. The large number of species centering in Mexico indicates a center of speciation in the Tertiary. *Pinus* subsect. *Cembrae* (ACD) is represented by five species of high altitudes and northern latitudes but is absent from Eastern North America, which lacks high mountains (Little & Critchfield, 1969, map 4). *Pinus albicaulis,* whitebark pine, is a timberline tree of the northern Rocky Mountains and the only New World member of the group. *Pinus cembra,* Swiss stone pine, grows at high altitudes in the Alps and Carpathian Mountains of southern Europe. The other three species are Asian: *P. sibirica,* Siberian stone pine, mostly in western and central Siberia; *P. pumila,* Japanese stone pine, from northwestern Asia to Japan; and *P. koraiensis,* Korean pine, from Korea to southeastern Siberia and Japan. This subsection has been regarded as one of the most primitive in the genus and is characterized by a closed cone.

Of similar distribution is a genus of birds, *Nucifraga,* related to jays and crows. These birds break open the cones and store and eat the large wingless seeds of sect. *Cembrae,* thus aiding dispersal. The New World species is *N. columbiana,* Clark's nutcracker or Clark's crow ("camp-robber"), and the Old World species is *N. caryocatactes,* European nutcracker, with ten named subspecies or races (Goodwin, 1976). Obviously, both pine and bird groups were present together in the ancestral Arcto-Tertiary forests and may have evolved in symbiosis. Both bird species have a somewhat varied diet including other seeds, berries, insects, and eggs and readily learn to eat foods of humans.

The disjunct genus *Magnolia* has eight species in eastern United States, about 18 others southward in tropical America, and about 50 in Eastern Asia south to Java (Little, 1971). Seven of the 11 sections of the genus are entirely Asian, two are wholly American, and two occur in both regions. Nine sections are confined to a single region.

The eight species of *Magnolia* in eastern United States are classified in four sections. *Magnolia acuminata* and a species of eastern China are in sect. *Tulipastrum,* sometimes treated as a genus. Two of the southern Appalachians, three of the Coastal Plain, and one of Mexico are placed with three of Asia in sect. *Rytidospermum. Magnolia virginiana* is sufficiently distinct to be alone in sect. *Magnolia. Magnolia grandiflora* of the southeastern Coastal Plain is the northern outpost of sect. *Theorhodon,* composed of about 16 evergreen tropical species south to Puerto Rico, the ancient flat-topped peaks of southeastern Venezuela, and Ecuador. All species of the last section may have evolved from the same New World ancestor.

Alnus, alder, is another illustration with widespread subgenera. *Alnus maritima* has an odd range in two areas more than 1,800 km distant: Coastal Plain in five counties of eastern Maryland and one in southern Delaware and stream banks on granite bedrock in two counties of southern Oklahoma. This pioneer species in wet soil bordering water is regarded as a relict of former wider range with the Oklahoma area the older of the two (Furlow, 1979: 17). It is the only New World representative of *Alnus* subg. *Clethropis,* which ranges also from Himalayas to Japan and as fossil records in Western North

America. *Alnus japonica* of Japan has been treated as a variety.

Trees of Western and Eastern North America

Relatively few tree species confined to North America have broad east-west ranges and can be classed as transcontinental. Examples are mostly species of wide occurrence in the northern coniferous forest, such as *Picea glauca, Larix laricina, Populus tremuloides,* and *Betula papyrifera.* Southward, the few tree species that are found across the treeless interior commonly grow in moist soil near water, for example, *Salix nigra* and *Acer negundo.*

Every field botanist traveling for the first time from Eastern to Western North America (or the reverse) has observed the striking resemblance of various trees and other plants to species previously studied. These similar plants are known as paired species, parallel species, species pairs, east-west vicarious taxa, and east-west vicariads. More than two species may be involved. Long lists of these species pairs have been compiled (Wood, 1971).

A few examples of tree species pairs may be noted, the western first: *Pinus monticola* and *P. strobus, Juniperus scopulorum* and *J. virginiana, Quercus gambelii* (also *Q. lobata* and *Q. garryana*) and *Q. alba, Celtis reticulata* and *C. occidentalis,* and *Acer grandidentatum* and *A. saccharum* (also *A. nigrum* and *A. barbatum*).

The explanation is obvious. The western and eastern forests became separated and isolated following western mountain uplifts and the origin of drier interior plains with grassland vegetation in late Miocene and early Pliocene more than five million years ago. One or both species of the pair changed during the interval though not into a distinct genus.

Relict Species

Some tree species of disjunct genera appear to be old and relict and declining, often rare. However, *Liriodendron tulipifera* and *Sassafras albidum* of Eastern North America are widespread and common. They are also the northernmost members of their families, Magnoliaceae and Lauraceae. Many species of conifers are rare or local in North America. Thirty-five, mostly western, have been the subject of a special publication with maps (Little, 1975).

Examples of relict tree species in Eastern North America with published maps (Little, 1971–81, vol. 4) include: *Cladrastis kentukea* (map 35); *Cotinus obovatus* (map 46); *Illicium parviflorum* (map 73); *Leitneria floridana* (map 74); and *Stewartia ovata* (map 147). Four tree species are endemic to islands of California, for example, *Lyonothamnus floribundus* (vol. 3, map 98) representing an endemic genus.

General observations made earlier on the ecology of rare plants may apply also to many examples of disjunct genera and species. Griggs (1940) concluded that a species is rare because it cannot compete successfully with common plants, that most rare species have habitats in the early stages of the ecological succession, and that many rare plants have disrupted ranges and are slowly dying out. Examples of trees characteristic of dry rock outcrops in the upland succession are *Cotinus obovatus* and *Torreya taxifolia* (Little, 1971–81, vol. 1, map 88-E). Trees of wet soil of stream banks in the lowland succession include *Leitneria floridana* (vol. 4, map 74) and *Alnus maritima* (vol. 4, map 8).

Minor geographic variations may be expected among isolated populations of ancient taxa. Most careful studies of conifers have revealed additional differences. In observing conifers for many years, I have noted some local variations and have named a few. Opinions disagree whether the differences should be designated as varieties or species or left unnamed. An extreme example is the genus *Cupressus,* cypress, which has been mentioned. As many as 15 New World species have been accepted, mostly with separate ranges (Wolf & Wagener, 1948). However, I distinguish only eight species, subdivided further into ten geographical varieties (Little, 1975, plate 9, maps 29–35). The species and varieties in western United States have ranges so local and disjunct that the isolated stations for each species have been counted. Clearly, these are relicts of former greater occurrence.

Discussion

Several observations are offered here. My interest in this subject goes back to a fascinating graduate course in floristics by an inspiring professor, Henry Chandler Cowles, at the University of Chicago (1927).

Progress in geology. Historical plant geography has kept pace with progress in geology. When I studied historical geology (1925), there was no precise time scale in millions of years. In

structural geology (1926), I was taught that continents and ocean basins were fixed and that continents moved up and down vertically (isostasy) but never horizontally. Alfred Wegener's hypothesis of continental drift proposed in 1915 did not come to the attention of plant geographers until later. I recall an introduction to the subject by Wendell H. Camp at a field meeting of botanists in 1939. Some botanists readily grasped movement of continents as more plausible than land bridges. Others hesitated momentarily, because physicists had no explanation or because the hypothesis seemed unnecessary. Now, continental movements provide an explanation for some problems of plant distribution! Recent acceptance of wandering poles will lead to additional explanations and may require revision of paleogeographic maps. The shift in pole position and earth's axis within the past 80 to 100 million years is estimated at about 20 degrees latitude (Good, 1964; Harrison & Lindl, 1982).

Time. One important concept in studies of plant geography is time. A century ago James (1881: 67) observed "that the time necessary for the distribution of our plants has been sufficiently long." He concluded also that the species of plants common to Europe and America had a common origin and migrated south. Time has been sufficient for many tree species to migrate to the most remote part of the earth wherever conditions for establishment are suitable. It is difficult to conceive of continuous time longer than the few thousand years of written history.

However, the time since the beginning of the Tertiary period, about 65 million years, is adequate to explain present distribution of trees and other seed plants throughout the world wherever there are suitable habitats. The time is ample for migration by any means, gradual, in steps, or by accident in long distance dispersal. Of course, continental movements speed the process.

Change. A key word in studying plant distribution is change, or dynamics. Just as all organisms end in death, all species become extinct or change into others by evolution. Likewise, the natural distribution of a species is slowly changing.

Persistence of tree genera. It seems remarkable that many extant or recent tree genera can be traced back as much as 50 million years into the Eocene epoch or doubtfully farther into the Cretaceous period. That is a very long time for a genus to maintain its identity and to continue to be common and widespread. In contrast, evolution of land vertebrates has been more rapid. Within the same time interval, *Equus,* the modern horse, developed from the 4-toed ancestral dawn horse, *Hyracotherium* (*Eohippus*). Even after separation of the land masses and forest regions in the Miocene roughly 15 million years ago, the tree genera in isolation maintained their identity. Obviously, these old tree genera are stable and have a slow rate of evolution.

Trees and herbs compared. Herbaceous plant species are considerably more numerous than trees in temperate regions though not as well preserved in the fossil record. Also, herbaceous species of wide distribution in temperate regions in both New and Old Worlds are much more numerous than trees, as noted above. However, many of the herbs are circumpolar across far northern regions above the tree line or climatic limit of trees. Thus, it appears that herbs have a more rapid rate of evolution than trees and that herbs migrate faster. Herbs have much shorter life cycles and more numerous generations and mostly small seeds adapted to long distance dispersal. While one seedling in many years replaces a tree, an annual herb is followed by another plant each year.

Conclusions. The relationships of North American trees with Eastern Asia have been overemphasized and are readily explained by earth changes accepted within recent years.

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DISTRIBUTION PATTERNS AMONG ARTHROPODS OF THE NORTH TEMPERATE DECIDUOUS FOREST BIOTA[1]

ROBERT T. ALLEN[2,3]

ABSTRACT

The distribution patterns of seven different arthropod taxa representing eleven individual monophyletic lineages with representatives in eastern North America, Europe, and northeastern Asia were analyzed. Taxon cladograms representing relationships among taxa were converted to area cladograms representing relationships among areas. Nine of the area cladograms were found to represent one congruent repetitive distribution pattern. The two remaining cladograms represented two additional independent distribution patterns. The distribution patterns were correlated with geological events that have alternately divided and reunited the principal land areas during the past 180 million years.

The largest and most diverse segments of the biota of the North Temperate Deciduous Forest presently occur in three disjunct areas: (1) eastern North America, (2) Europe, and (3) northeastern Asia. This has been known for almost one hundred and forty years. What is not known is the definitive relationships of these three related biotas to one another or the relationships of these biotas to other, perhaps more distantly related biotas. To establish definitive relationships among biotas one must practice a science of comparative systematic biology and employ an objective methodology.

The objective of this paper is two-fold. First, an objective comparative methodology will briefly be outlined whereby biotas may be analyzed and definitive relationships established. Second, a number of monophyletic, arthropod taxa occurring in North America (NA), Europe (EU), and northeastern Asia (AS) will be analyzed to determine the cladistic and biogeographic patterns of these taxa.

AN OBJECTIVE METHODOLOGY FOR COMPARATIVE SYSTEMATIC STUDIES

Let us consider how we might compare the biotas of the three areas under consideration. We might begin by making lists of the similar endemic taxa common to two or more areas. A number of such lists have been made. Asa Gray (1846) made such a list and recorded a number of plant species and higher taxa that were endemic to eastern North America and Japan. Some one hundred years later Li (1952) reanalyzed the floristic similarities between eastern North America and northeastern Asia in the light of modern systematic botanical data. These new data, presented by Li, showed that the species Gray had thought to be the same in the two areas were, in fact, different species. Li did, however, record 52 genera that were endemic to eastern North America and northeastern Asia. A number of additional papers (Graham, 1972) since the work of Li have further documented the similarities of the floras in these two areas.

Similar studies comparing the biotas of Eastern North America and Europe have also been published. Lindroth (1957) presented a comprehensive list comparing the faunas of the arctic. boreal, and temperate regions of North America with comparable areas in Europe. The symposium papers contained in Löve and Löve (1963) also document the similarities of the biotas of the North American and European continents. Numerous additional papers, particularly those of a taxonomic nature treating taxa common to North America and Europe, give examples of taxa with disjunct distributions on the two continents.

Studies comparing the biotas of Europe and northern Asia or comparing the biotas of Europe. northern Asia, and North America are limited. The work of Hara (1952, 1956) does compare the plants of the three areas. But the majority of the published literature compares only two of the

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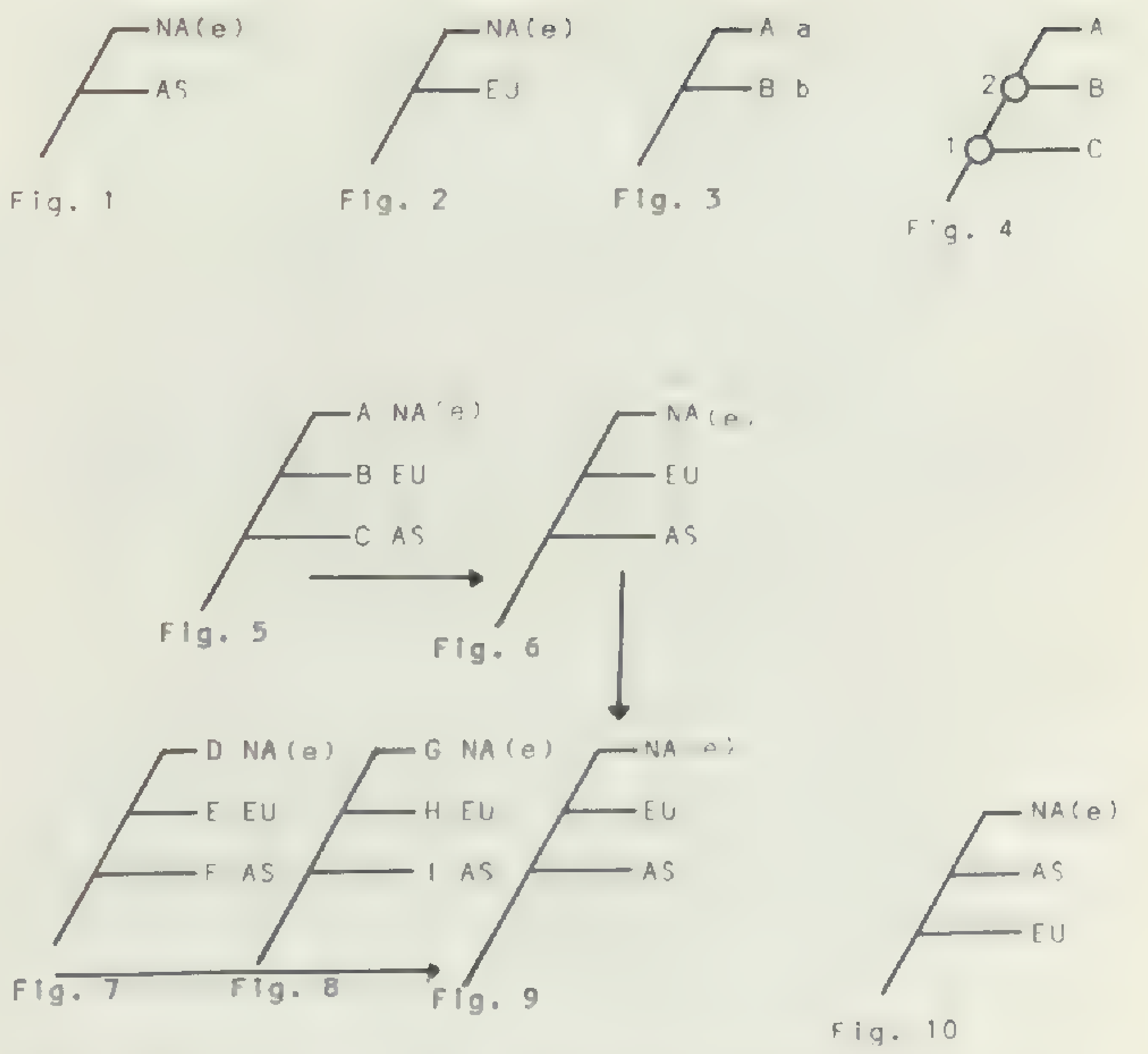
areas and we may be able to form only two sets of comparative statements: (1) the biota of NA(e) (North America, east) is related to the biota of AS (Asia) (Fig. 1) and (2) the biota of NA(e) is related to the biota of EU (Europe) (Fig. 2). These statements may be considered two-entity comparisons and as such have "low" informational content (Platnick & Nelson, 1978).

Since two-entity statements are prevalent throughout systematic biological literature it is important to clarify the statement just made, i.e., that two-entity statements have "low" informational content. In systematic biology two-entity statements may be of two types: (1) two-taxon statements—species A is related to species B; (2) two-area statements—the biota of area *a* is related to the biota of area *b* (Fig. 3). If one accepts the idea that extant taxa come from preexisting taxa through a series of interconnected, related ancient ancestors, i.e., evolution, then all taxa and biotas are related to one another at some level. The question, then, is at what level the two taxa or biotas are related. To answer this question, a third entity must be considered so that a comparative statement may be formed.

Consider the proposition that A and B are more closely related to one another than either is related to C (Fig. 4). This is a three-entity comparative statement with a higher informational content than the two-entity statement. In an evolutionary context we may see that A and B shared a more recent common ancestor, hypothetical ancestor 2, than either did with C, and C's hypothetical ancestor 1 (Fig. 4). We may also deduce that A and B share one or more attributes in common that are not shared with C.

If the discussion just given seems too simple for the advanced student or practitioner of systematic biology, consider the published literature. This body of information is replete with example after example of two-entity statements. If we are to move toward an objective, analytical format in systematic biology as suggested by Ian Ball (1975), we must begin constructing comparative statements composed of a minimum of three entities.

The construction of a comparative three-entity statement in systematic biology begins with a cladistic analysis of three or more taxa believed to have a monophyletic relationship. The methods and procedures for executing a cladistic analysis have been discussed at length by a number of authors including Hennig (1966), Ross (1974), Crisci and Stuessey (1980), and Wiley (1982).



FIGURES 1–10. 1–2. Two area statements illustrating the relationships between North America east (NA(e)), Asia (AS), and Europe (EU).—3. A two taxon statement illustrating the relationships between hypothetical species A, and B occurring in *a* and *b*.—4. A three taxon statement illustrating the relationships between hypothetical species A, B, and C.—5. A cladogram of relationships existing among hypothetical species A, B, and C occurring in eastern North America, NA(e), Europe, EU, and Asia, AS.—6. An area cladogram derived from Figure 5 illustrating the relationships among three disjunct geographical areas.—7–8. Taxon/area cladograms of two hypothetical monophyletic lineages.—9. An area cladogram depicting the congruent distributional patterns illustrated in Figures 6, 7, and 8.—10. An area cladogram illustrating a second type of distributional pattern that might exist between eastern North America, NA(e), Asia, AS, and Europe, EU.

Here we need only note that there are four basic tenets necessary for a cladistic analysis of any taxon: (1) an analysis and comparison of characters and character states in the taxon being studied and in suspected related taxa; (2) the postulation of apomorphic (derived) and plesiomorphic (ancestral) states for as many characters as possible from the analysis and comparison of character states in the study group and related groups; (3) the establishment of relationships (monophyletic lineages) based on the possession of shared apomorphic characters and the graphic illustration of these relationships in the form of a taxon cladogram; (4) an analysis of the biogeographic relationships of the taxa and the areas in which they occur by converting the taxon cladograms to area cladograms. Let us consider a hypothetical example in which we cladistically and biogeographically analyze a monophyletic taxon with representatives in three disjunct areas.

Let us suppose that we discover a genus with representatives in each of the three disjunct north temperate deciduous forest areas: species A, NA(e); species B, EU; species C, AS. Let us also suppose that by applying the methodology for determining cladistic relationships we determine that species A and B are more closely related to one another than either is to species C. This information concerning relationships may be expressed in the form of a taxon cladogram (Fig. 5). This taxon cladogram is a statement that fulfills the following three requirements for a scientific hypothesis (Ball, 1975): (1) the cladogram fits the known data about relationships; (2) the cladogram may be tested by a reanalysis of the known data and/or the discovery of new character state data; (3) the cladogram predicts that the relative relationships of the three known taxa will remain the same no matter how many additional species may be discovered, i.e., species A and B will always share a more recent common ancestor with one another than either will ever share with species C.

Once the cladistic relationships of a monophyletic lineage have been established, other types of data, for example distributional data, may be plotted against the cladogram. Rosen (1975, 1978) and Nelson and Platnick (1981) have discussed the methodology as well as the scientific basis for converting taxon cladograms into area cladograms by plotting distributional data on the taxon cladogram. When this distributional data is plotted on the cladogram (Figs. 5, 6), we may see that we have a hypothesis relevant to the relationships of the three disjunct areas in which species A, B, and C occur: eastern North America [NA(e), species A] and Europe [EU, species B] have shared a more recent common biota with one another than either area has shared with northern Asia [AS, species C] (Fig. 6). Using this methodology, it is necessary for a worker to make only two assumptions: (1) that extant organisms have evolved from preexisting organisms and (2) that extant species have evolved due to an allopatric speciation model.[4] Note that the hypothesis does not involve nor suggest mandatory, long-distance dispersal.

The hypothesis about the relationships of biotas in NA(e), EU, and AS may be tested in at least two ways. It has already been suggested that the taxon cladogram may be tested by the further study of the characters on which the cladogram is based and the study of additional characters not previously used. In addition to this test on character states, a search may be made for additional monophyletic taxa with a distribution range similar to the first taxon. If such taxa are discovered, taxon cladograms may be deduced (Figs. 7, 8) and these taxon cladograms may be converted into area cladograms (Fig. 9). If the area relationships of the new, additional taxa are the same as the first taxa, the hypothesis is corroborated and may suggest a generalized distribution pattern (Fig. 9). If the new, additional taxa suggest a different set of area relationships (Fig. 10), then the original hypothesis may be incorrect or a second distribution pattern may exist. In either case, corroboration of the first hypothesis may be objectively pursued.

Once corroborated and generalized distribution patterns emerge, we may consider the phenomena that have contributed to the evolution of these patterns. We might ask, "Are the patterns due to the dispersal of organisms across pre-existing barriers and to the subsequent isolation and evolution of the organisms?" or "Are the patterns due to historical factors that divided ancient cosmopolitan populations and set the stage for allopatric speciation to occur?" Before attempting to answer these questions, let us consider the literature that is available and search for taxa that are informative about biotic relationships between NA, EU, and AS, and describe how we can fit the available information into the objective methodology that has been outlined.

USING PUBLISHED DATA IN A CLADISTIC-BIOGEOGRAPHIC ANALYSIS

To objectively analyze distribution patterns, two prerequisites are necessary: (1) a monophyletic taxon with distinct taxa, endemic to three or more areas and (2) a taxon cladogram or data from which a taxon cladogram may be postulated. These two prerequisites may be satisfied through original research or, in some instances, by utilizing previously published information. The analysis of north temperate distribution patterns presented in this paper relies heavily upon the work of other authors. These previously published data are not always in a form that can be directly used in a cladistic biogeographic analysis

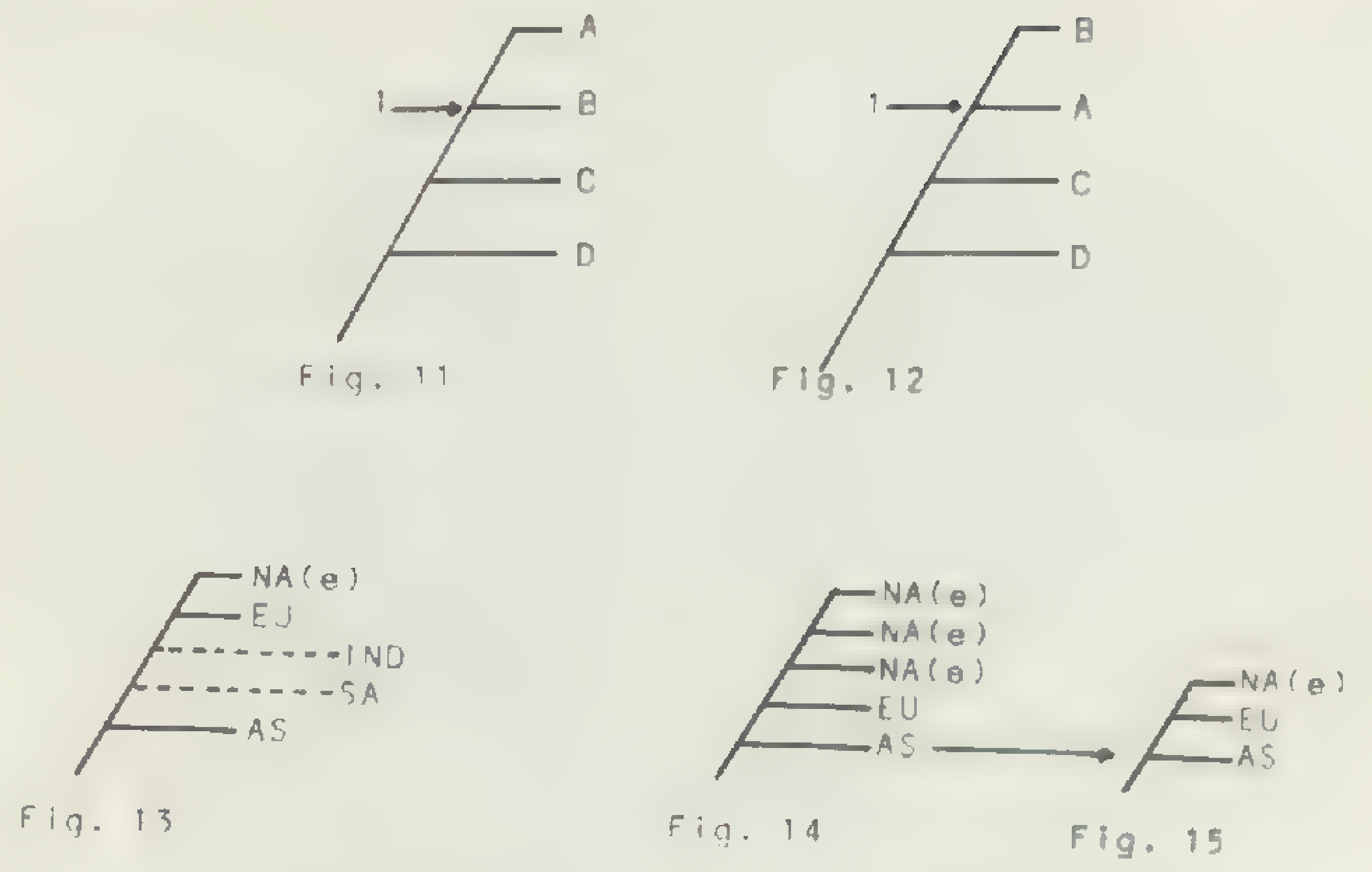
[4] I fully realize that perhaps one-third of the plant species (as well as some animal taxa) have originated due to processes other than allopatric speciation. Nevertheless allopatric speciation does appear to be a viable process that plays an important role in the origin of many animal species including the taxa discussed in this paper.

and some rearrangement of the data is necessary. The following is a brief statement of how previously published data used in this paper are adapted in order to perform a cladistic-biogeographic analysis. Three subject areas need to be considered: (1) the conversion of phylogenetic diagrams to cladograms; (2) the conversion of taxon cladograms to area cladograms; and (3) the accuracy of distribution records.

Diagrams representing the relationships of taxa to one another have been a part of systematic literature since the time of Haeckel (1866). These diagrams have been referred to by a variety of names, but the most common name appears to be "phylogenetic tree." More recently (1960s to the present), the diagrams have been referred to as cladograms.

It has only been within the past thirty years that definitive and objective methods have been proposed for the construction of cladograms. Central to this methodology is the establishment of relationships based on the possession of shared apomorphic (derived) characters. The validity of previously published phylogenies or cladograms stands or falls on whether or not the author postulated relationships based on shared apomorphic characters. In those instances where the method of determining relationships is clear, one may proceed with the use of the cladistic and distributional information. Frequently it is difficult to determine what method an author used to determine relationships. In those instances where the method of determining relationships is unclear or where relationships are based on some factor other than the possession of shared apomorphic characters, the published data is better left to rest in peace.

Relationship diagrams have also been published in a variety of formats. In this paper all of these formats have been changed to a single type of branching diagram. The use of a single format is extremely helpful in searching for and detecting redundant distribution patterns. In no case have the original data been changed, i.e., the relative relationships of all taxa (those taxa at the ends of the diagram branches) have not been changed. For example, in a diagram representing the relationship of four taxa A, B, C, and D (Fig. 11) where A and B are more closely related to one another than either is to C or D, and where A, B, and C are more closely related to one another than they are to D, the positions of the taxa have been scrupulously maintained. However, in some instances the location of taxa at terminal nodes, in this case A and B, have



FIGURES 11–15. 11–12. Taxon cladograms of a hypothetical group of species in which the positions of species A and B are reversed by rotating the cladogram at node 1. Such a rotation does not change the informational content of the cladogram.—13. An area cladogram in which the relationships of areas outside of North America, Europe, and Asia have been indicated by a dashed line.—14–15. Area cladograms illustrating how three species occurring in eastern North America, NA(e), have been reduced to one area in Figure 15.

been reversed (Fig. 12). Such a reversal has absolutely no effect on the interpretation of the data presented. The statement "A and B are more closely related to one another than either is to C" is the same as the statement "B and A are more closely related to one another than either is to C." Put in another way, nodes in a cladogram may be rotated on their axes. As you will see, this rotation procedure is often helpful in detecting congruent distribution patterns.

At this point it is worthwhile to remember that the plants and animals we study are not obliged to fit precisely and neatly into either our classification systems or our distribution patterns. Any student of nature, even after a limited amount of experience, quickly recognizes the variation that is rampant in nature. This does not mean that biological patterns do not exist, for certainly they do. It does mean that while striving to detect patterns that are common to large groups of taxa, we must also accurately record the variability we observe in nature. Patterns exist because individual plant and animal species have not evolved independently of one another. Individual species are constituent members of larger biotas. These biotas have shared common elements in their histories and it is these common elements for which we are searching. With these thoughts in mind I have employed two methodological procedures that have assisted in discovering common distribution patterns between the biotas in North America, Europe, and northern Asia.

The first methodological procedure that I have

used was necessary because many taxa occur in disjunct areas other than those under consideration. For example, Li (1952) noted a number of temperate deciduous forest taxa that occur not only in eastern North America and northeastern Asia but also in more southern tropical areas such as the Philippines. Other taxa such as some caddisflies (Insecta: Trichoptera) occur in eastern North America, Europe, northeastern Asia, India, Africa, etc. In the cladograms used in this paper, the relationships of taxa and areas outside of NA, EU, and AS have been indicated by dashed lines (Fig. 13). It is felt that this method conveys all of the known data about the groups but allows one to perceive what the relationships are among the areas and taxa that occur in our three principal areas, NA, EU, and AS.

The second methodological procedure used in detecting distribution patterns was first employed by Rosen (1975, 1978). In this technique, identical areas that are juxtaposed to one another in a single monophyletic lineage are combined (Figs. 14, 15). When this combining method is used, the original data should always be presented so that other workers will have access to all the facts and so that any conclusions may be judged objectively.[5]

The last topic to be considered here is the accuracy of distribution records. What is meant by accuracy is the tendency that some biogeographers had in the past to list taxa as occurring in broad geographical areas, i.e., Asia, North America. We now know that many of the geographical areas formally recognized as single units are actually composed of two or more geographical subunits. These subunits have often had independent and therefore different histories. Even the relatively small island of Celebes is composed of at least two independent island masses that only fused together a few million years ago. When summary cladograms of other workers have been used in this paper, the distribution of each taxon and lineage has been verified and determined as accurately as possible. This has sometimes led to conclusions that differ from those expressed by the original authors.

Using a cladistic methodology, including the methodological procedures just discussed, the distribution patterns of a number of north temperate, disjunct, monophyletic arthropod taxa have been analyzed. Let us consider these individual taxa, their taxon cladograms, and their area cladograms.

Taxon and Area Relationships Among Disjunct North Temperate Arthropod Groups

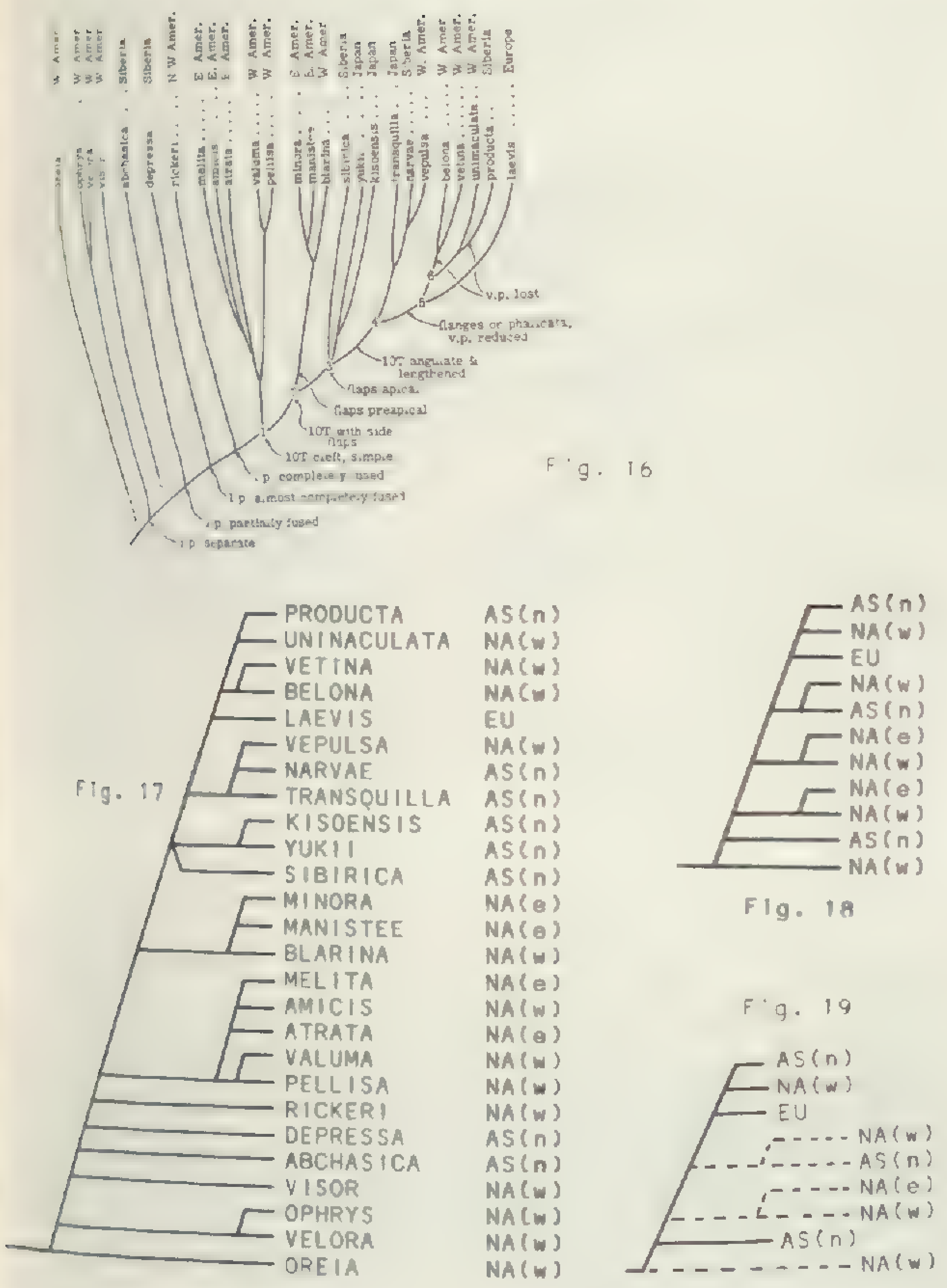
A search of the literature revealed a number of arthropod taxa with distributions that might be informative about the relationships of temperate biotas and areas in North America, Europe, and northeastern Asia. These groups occur in three orders of insects: the caddisflies (Trichoptera), the leafhoppers (Homoptera), and the beetles (Coleoptera), and in one group of spiders (Araneae).

caddisflies (insecta: trichoptera; glossosomatidae, philopotamidae, rhyacophilidae)

Caddisflies are a moderately large order of aquatic insects. The systematics and ecology of these organisms have attracted the attention of a number of highly competent entomologists for many years. One of the leading authorities of caddisfly systematics was H. H. Ross. Ross was especially interested in the basic taxonomy and biogeography of these insects.

Caddisfly taxa inhabit a wide range of aquatic habitats, but many taxa are characteristic of mountain regions throughout the world. Ross made a special study on the systematics of a number of mountain caddisfly taxa with worldwide distribution patterns and published the results in 1956. The phylogenetic diagrams that Ross presented for the mountain caddisfly taxa (Fig. 16) have been changed to taxon/area cladograms (Fig. 17). These cladograms, in turn, have been reduced to more simple cladograms (Figs. 18, 19) illustrating the area relationships between North America (NA) (east and west), Europe (EU), and Asia (AS). Four mountain caddisfly

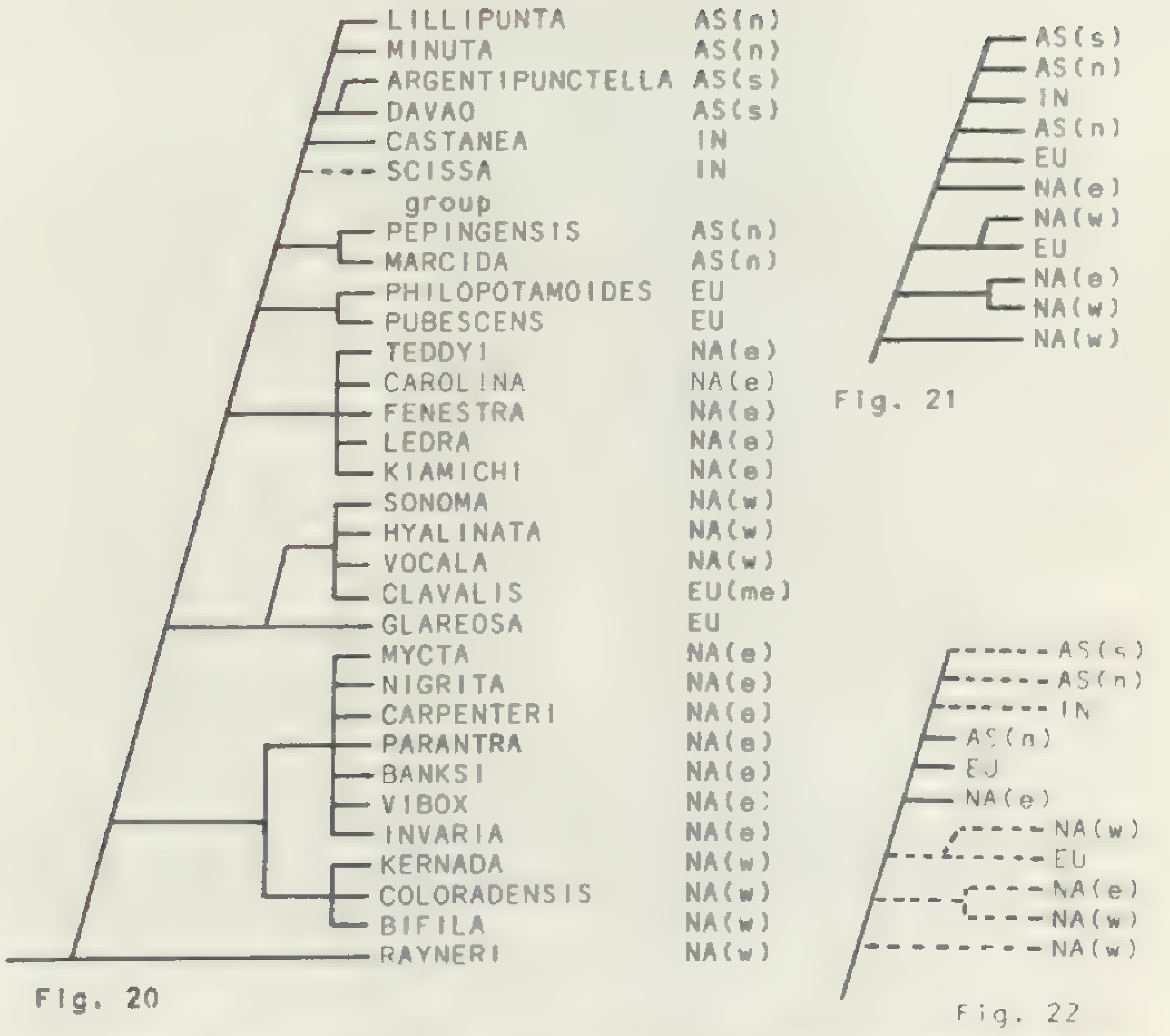
[5] At the first annual meeting of the Willi Hennig Society in 1980 Norman Platnick pointed out that Rosen's method of combining the same juxtaposed areas in a cladogram could have a negative result if the areas proved to be actually disjunct. Platnick believes that unless the combined areas represent the same natural areas of endemism (not disjunct), then one could argue that the "agreement" in different cladograms might result from chance alone. Perhaps Platnick's argument is true. However at our present level of knowledge it appears that there are both large (continents) and small (a mountain top) areas of endemism and that these areas of endemism have different levels of relationships (Allen, ms.). As long as the original, detailed data are presented accurately we will be able to return to the problem Platnick suggests exists if necessary.



Figures 16–19. The caddisfly genus *Rhyacophila sibirica* group.—16. Original phylogenetic chart published by Ross (1956).—17. Taxon/area cladogram based on Ross.—18–19. Reduced area cladograms.

taxa discussed by Ross (1956) that have representatives in the north temperate areas are being considered here. The four taxa and their associated taxon/area cladograms are as follows: (1) *Rhyacophila sibirica* group (Figs. 16–19), branch 6 (Figs. 20–22); *Glossosoma* (Figs. 23–25); (3) *Wormaldia* (Figs. 26–27); (4) Agapetini (Figs. 28–30).

When each of the reduced area cladograms representing the independent monophyletic lineages is considered (Figs. 31–36), two distribution patterns seem to be identical: the pattern in the *Rhyacophila sibirica* group (Figs. 31, 37) and the pattern in *Glossosoma* (Figs. 34, 40). We might now ask, "Are the other patterns in these north temperate caddisfly taxa radically different from one another?" When the area cladograms are considered (Figs. 31–36) the area sequences do seem to be different on the one hand, yet on the other hand there also appears to be some degree of congruence. Consider how the different patterns may be arranged in linear sequences (Figs. 37–42). Now consider how these linear sequences may be arranged so that the same areas correspond with one another (Fig. 43). This latter arrangement (Fig. 43) of the linear sequences in

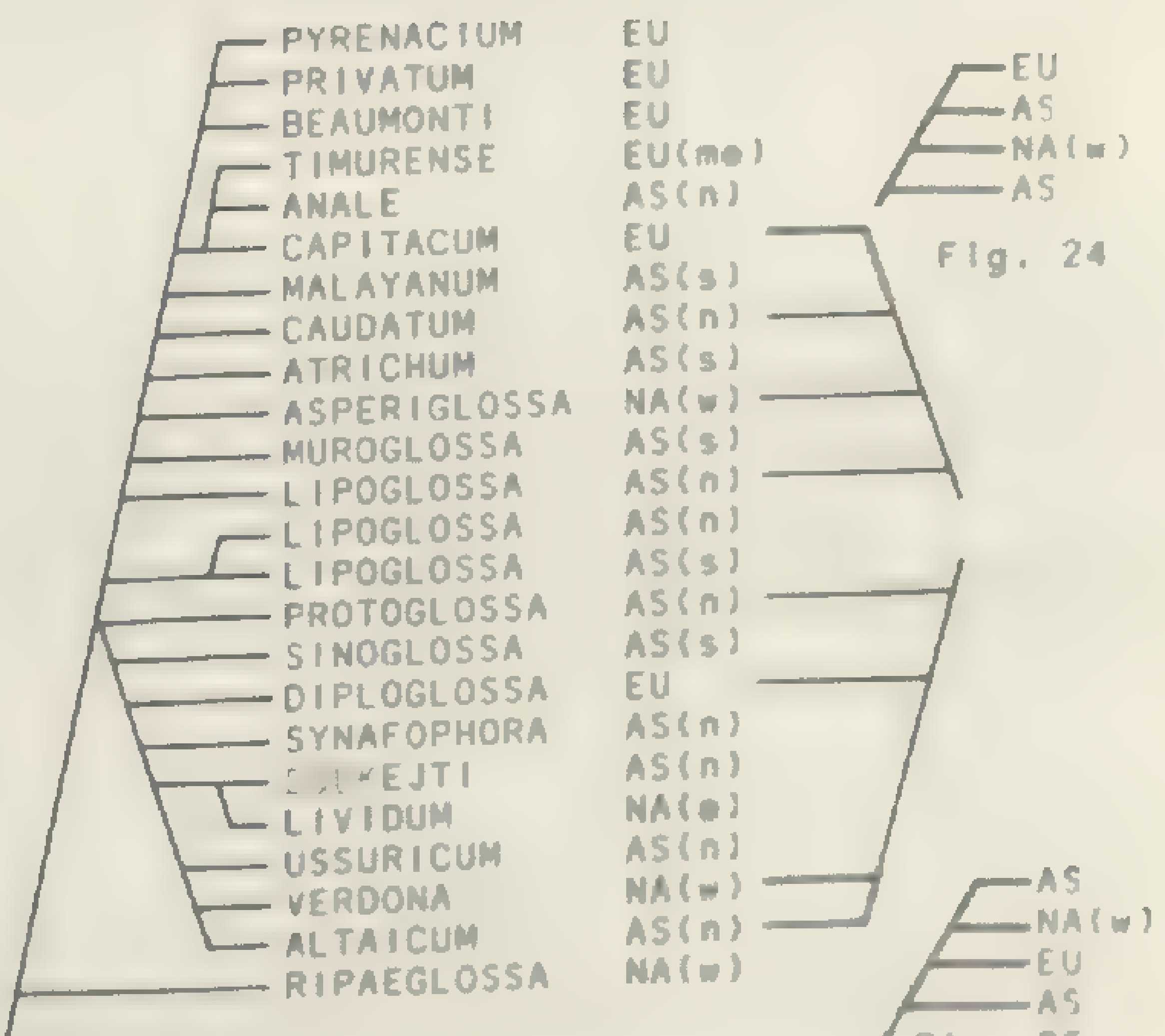


Figures 20–22. The caddisfly genus *Rhyacophila* branch 6.—20. Taxon/area cladogram.—21–22. Reduced area cladograms.

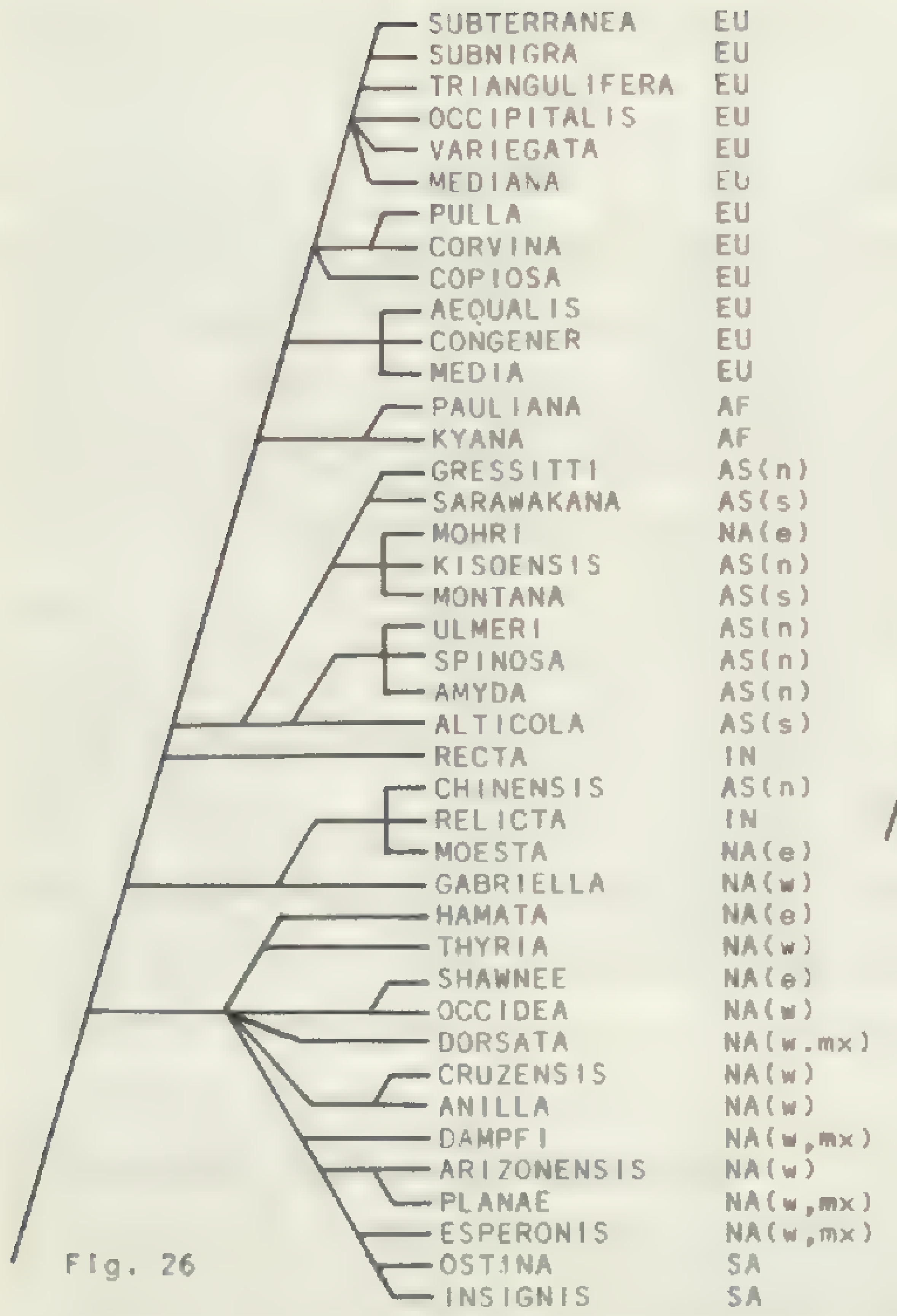
no way changes the original data but it does accentuate congruent areas and it notes those areas in which members of a monophyletic lineage do not occur. Perhaps we are seeing in each of the individual area cladograms a segment of a larger, more inclusive pattern (Fig. 44). Let us consider additional taxa.

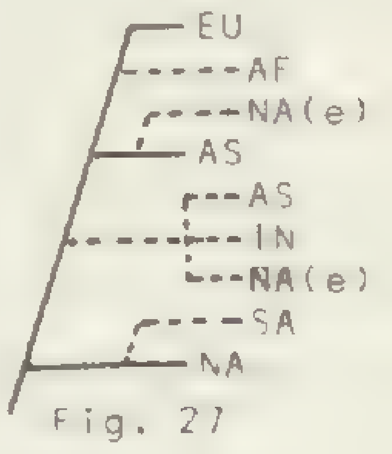
LEAFHOPPERS (INSECTA: HOMOPTERA; CICADELLIDAE)

Because of his general interest in the evolution and biogeography of insects, H. H. Ross worked on a number of diverse groups. In addition to the caddisflies, leafhoppers, especially the genus *Empoasca* (Cicadellidae), were of interest to Ross. He published a number of papers dealing with

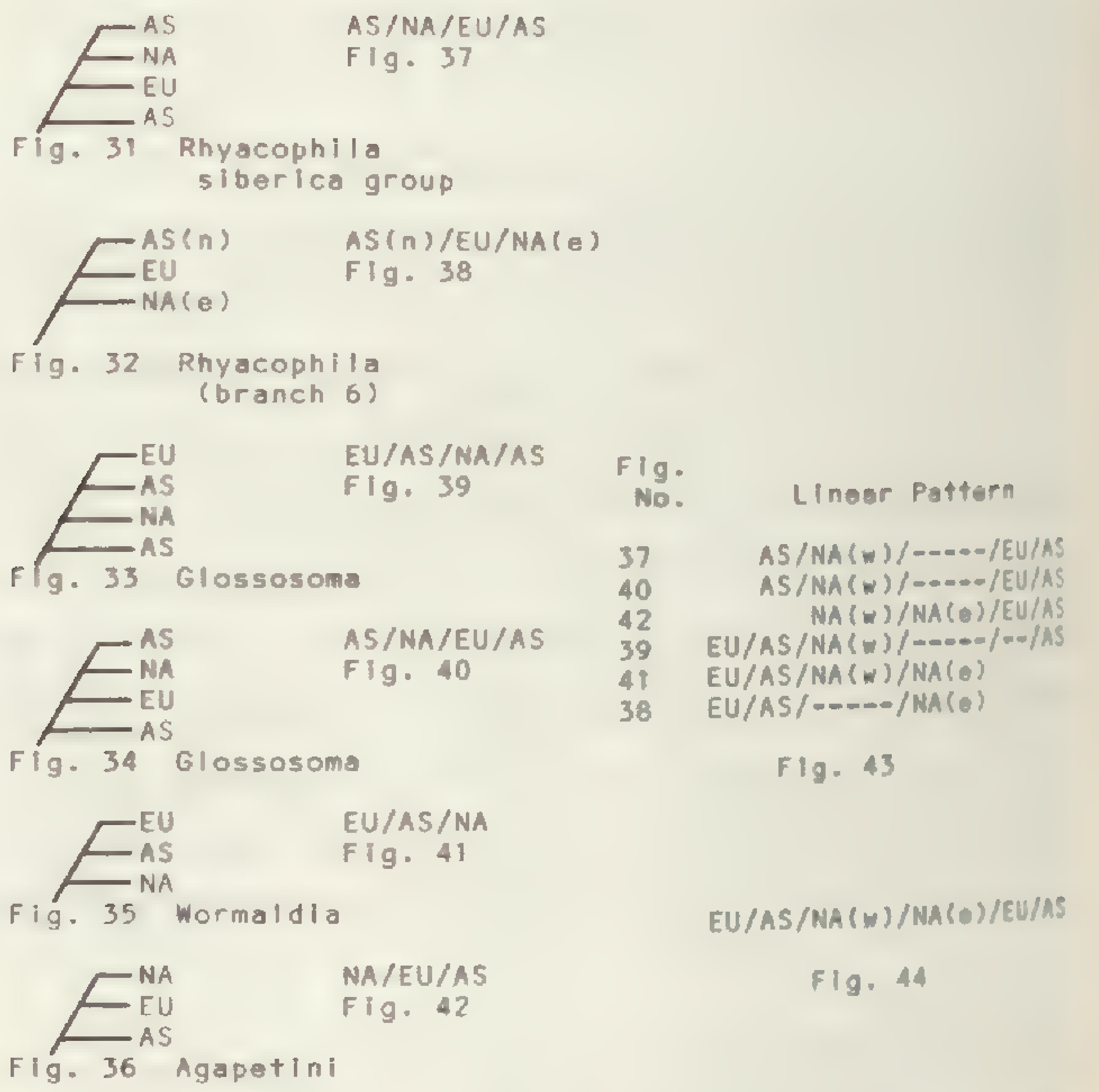


Figures 23–25. The caddisfly genus *Glossosoma*.—23. Taxon/area cladogram.—24–25. Reduced area cladograms.





FIGURES 26–27. The caddisfly genus *Wormaldia*.—26. Taxon/area cladogram.—27. Reduced area cladogram.

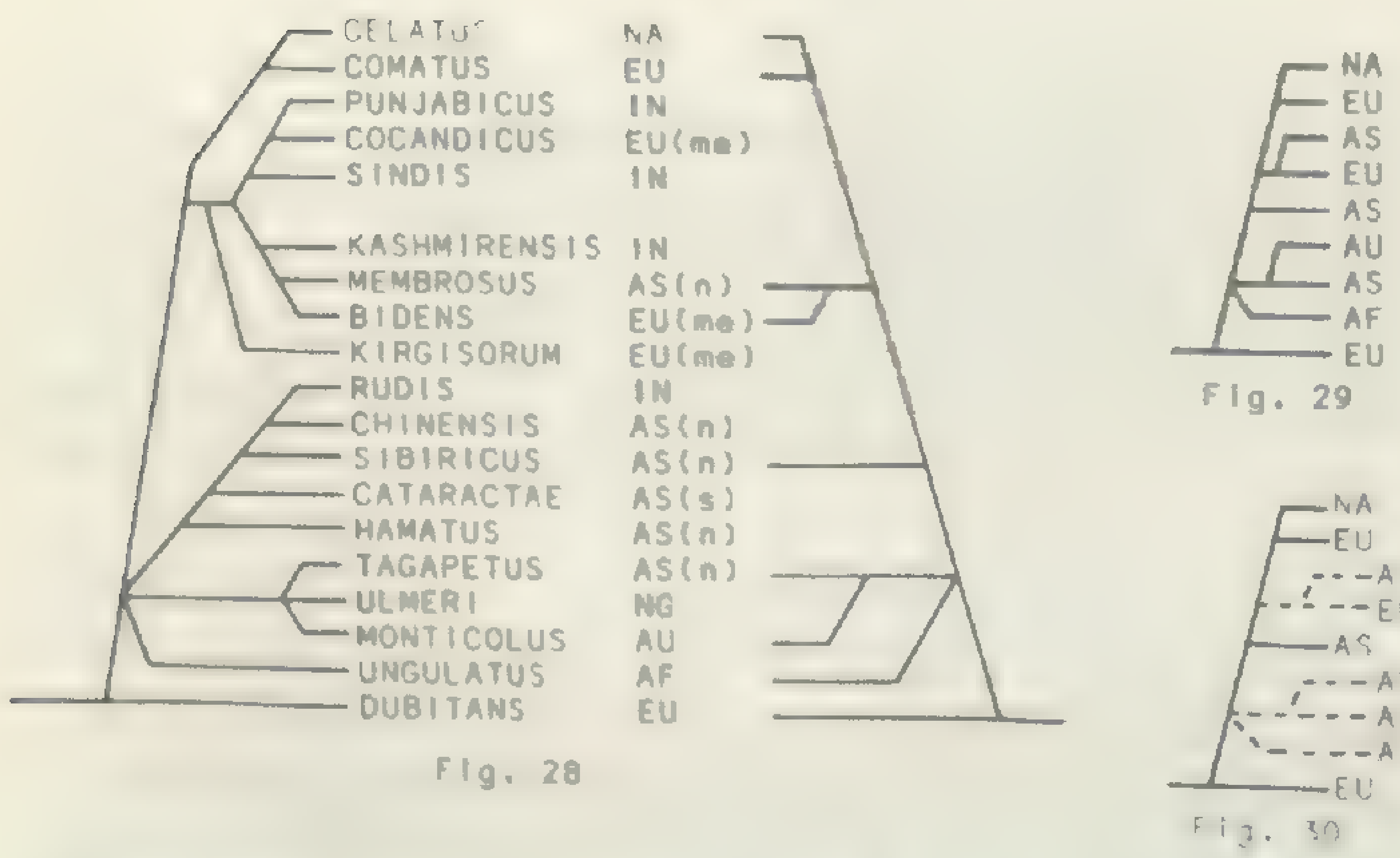


FIGURES 31–44. 31–36. Reduced area cladograms of the caddisfly taxa indicated.—37–42. Linear sequential arrangements of the areas occurring in reduced area cladograms.—43. Comparison of the linear sequential arrangement patterns in six monophyletic caddisfly taxa.—44. A generalized distribution pattern suggested by comparison of the six monophyletic caddisfly taxa in Figure 43.

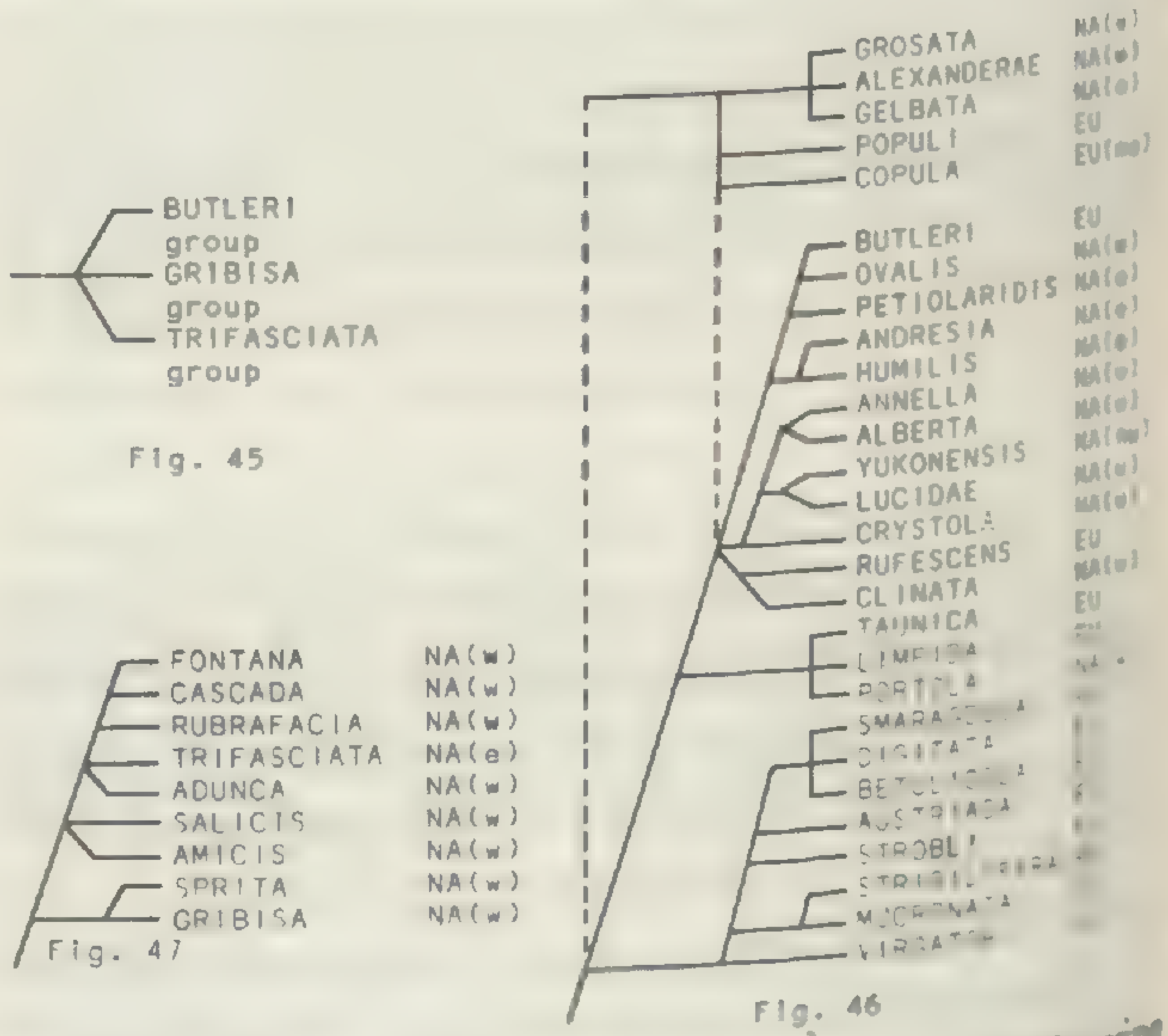
this genus. One of these papers is a taxonomic and biogeographic treatment of the empoascan subgenus *Kybos* (Ross, 1963).

Discussing the distribution of the subgenus *Kybos*, Ross said, "Of the 62 species of *Kybos* available for study, 49 are known only from North America, 13 from Europe. It would seem certain that species of this subgenus occur in Asia also, but currently none are available from that area, either through the avenues of specimens or descriptions giving details of male genitalia. When these distributions are plotted on the family tree for the subgenus, chart 1 [Fig. 46], it is remarkable that all of the known European species occur in the large branch containing the *butleri* and *copula* groups."

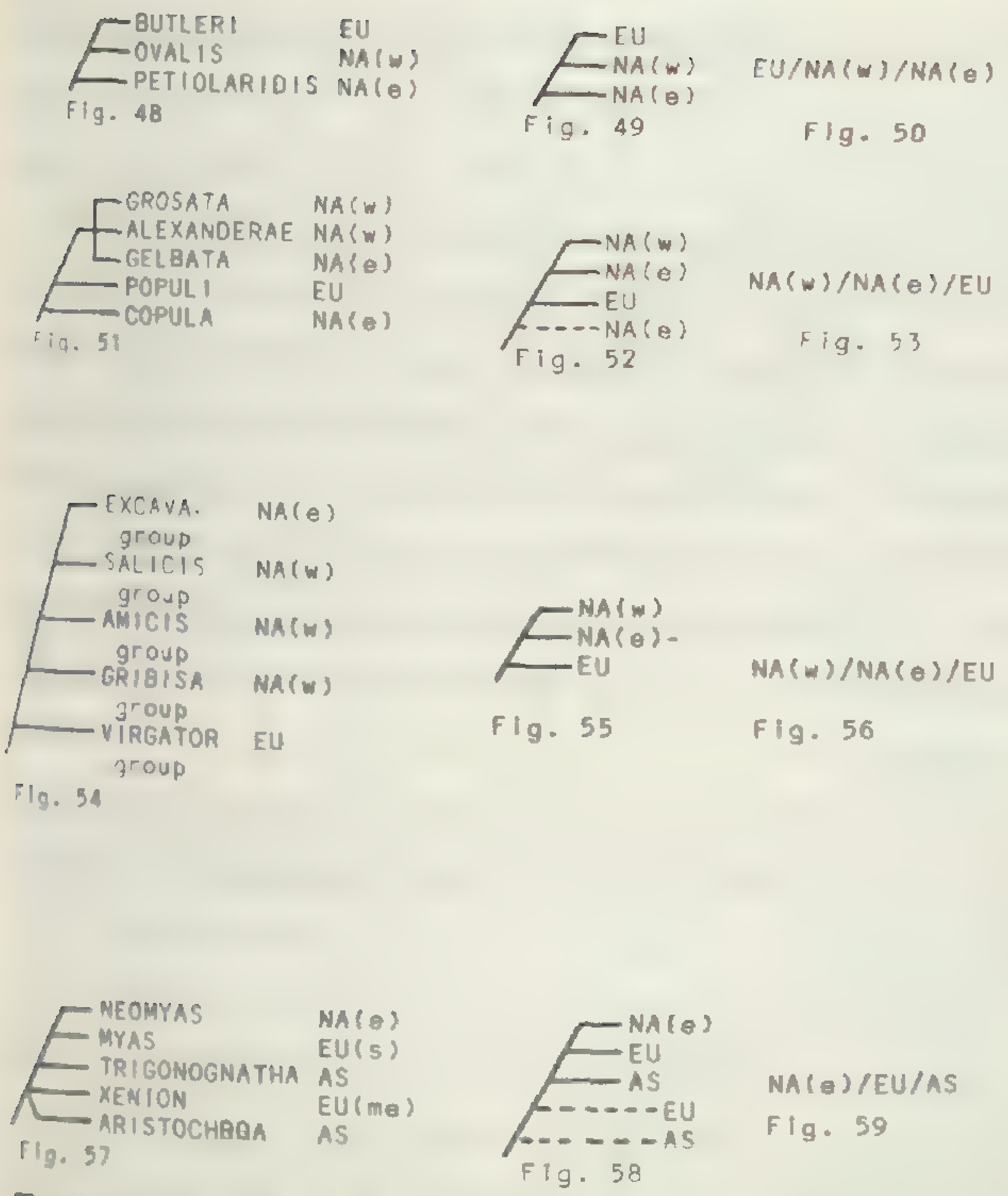
Unknowingly, Ross alluded to the fact that *Kybos* is a north temperate taxon and that representatives might well occur in northeastern Asia. Ross had certainly seen many examples of this type of Northern Hemisphere distribution



FIGURES 28–30. The caddisfly tribe Agapetini.—28. Taxon/area cladogram.—29–30. Reduced area cladograms.



FIGURES 45–47. 45. A taxon cladogram showing an unresolved trichotomy existing between the three major groups in the leafhopper subgenus *Kybos*.—46–47. Taxon/area cladograms of the species taxa in the *butleri* (Fig. 46), *gribisa*, and *trifasciata* (Fig. 47) groups in the subgenus *Kybos*.



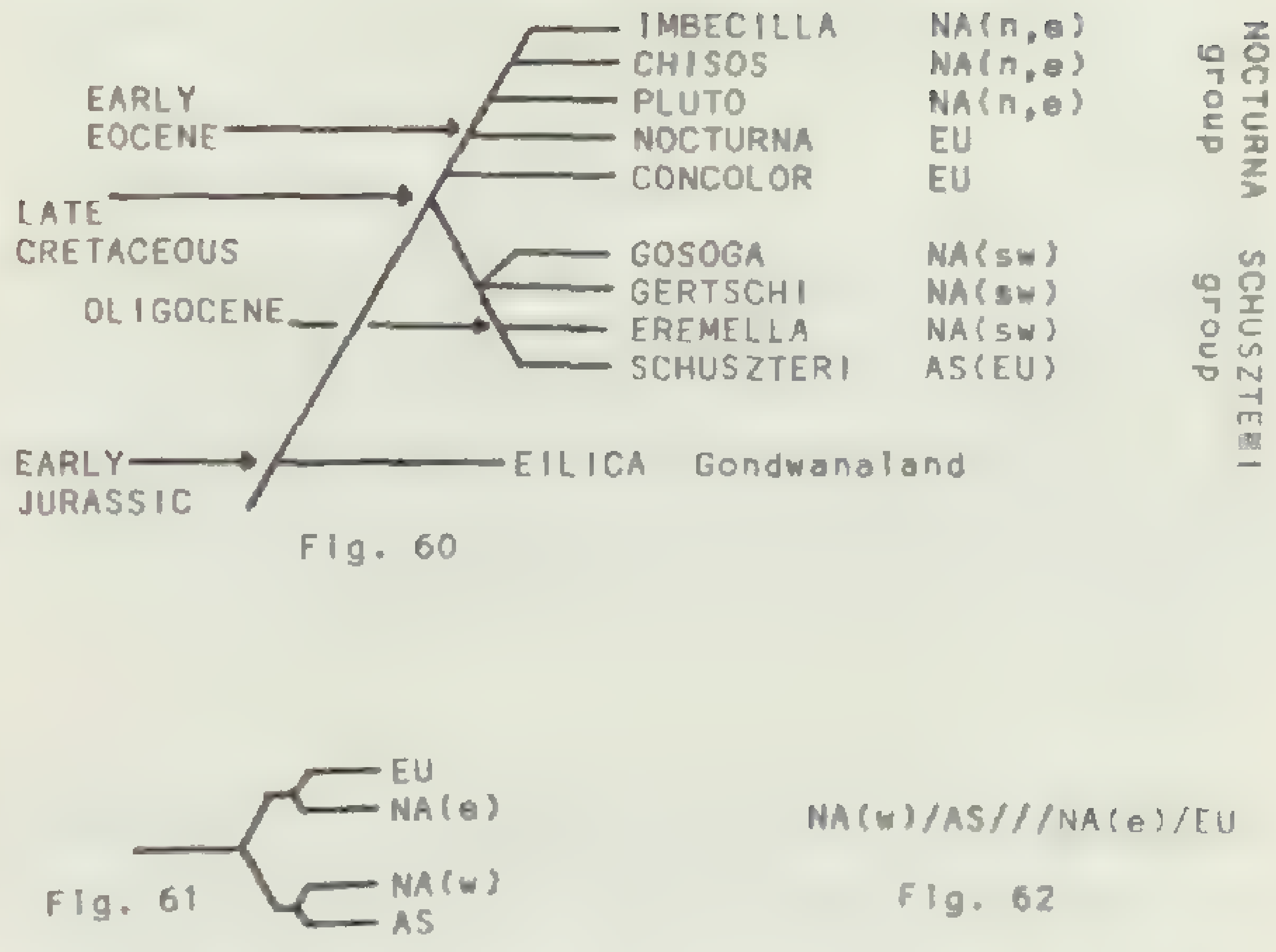
FIGURES 48–59. 48, 51, 54. Taxon/area cladograms of three lineages in the subgenus *Kybos*.—49, 52, 55. Reduced area cladograms of three *Kybos* lineages illustrated in Figures 48, 51, and 54.—50, 53, 56. Sequential linear arrangement of area cladograms of three *Kybos* lineages illustrated in Figures 49, 52, and 55.—57. Taxon/area cladogram of the genera in the ground beetle subtribe Myadi.—58. Reduced area cladogram of the subtribe Myadi.—59. Sequential linear arrangement of the reduced area cladogram of the subtribe Myadi.

from his work with caddisflies. It will be interesting to see where any north Asian species fit in the cladogram should they be discovered in the future.

If the major species lineages in *Kybos* are determined and the distribution ranges are plotted against these lineages (Figs. 45–47), there appear to be three lineages (Figs. 48, 51, 54) that are informative about north temperate area relationships: *Kybos* lineage 1 containing *butleri* and two other species (Figs. 48–50); *Kybos* lineage 2 containing the *copula* lineage (Figs. 51–53); and *Kybos* lineage 3 containing the *trifasciata* lineage, plus the European species that occur in the major *butleri* group (Figs. 54–56). Before considering the possibility that these three leafhopper patterns (Figs. 50, 53, 56) are congruent with the caddisfly pattern (Fig. 44) let us examine patterns in two additional arthropod groups.

GROUND BEETLES (INSECTA: COLEOPTERA; CARABIDAE)

The ground beetle family Carabidae is worldwide in distribution with a significant fauna in



FIGURES 60–62. 60. Taxon/area cladogram of the spider genus *Callilepis*.—61. Reduced area cladogram of the genus *Callilepis*.—62. Sequential linear arrangement of the reduced area cladogram of the genus *Callilepis*.

North America, Europe, and northeastern Asia. A number of monophyletic taxa in this north temperate fauna have disjunct representatives in NA(e), EU, and AS. To date, only one taxon, the subtribe Myadi, has been objectively analyzed (Allen, 1980).

There are six genera in the subtribe Myadi: *Neomyas*, North America; *Myas*, Europe; *Xenion*, southern Europe; *Aristochroa*, Tibet-China; *Trigonognatha*, China, Japan, Korea, Formosa; and *Steropanus*, China. Specimens of *Steropanus* have not been available for study and therefore the genus is not discussed. A cladogram depicting the relationships of these taxa with their distributions has been constructed (Fig. 57). Unfortunately, there remains an unresolved trichotomy at the base of the cladogram, but this does not detract from the information content above this node (Fig. 58). We may see that in the Myadi, North America and Europe appear to have been more recently associated with one another than either area was with Asia (Figs. 57–59).

SPIDERS (ARANEAE: GNAPHOSIDAE)

Platnick (1975a, 1975b, 1976) has analyzed the cladistic and biogeographic relationships among species in the spider genus *Callilepis*. *Callilepis* is presently found in North America (east and west) and in Europe reaching east into northeastern Asia. This distribution pattern, at first glance, may not appear to be disjunct between Europe and Asia, but when the ranges of the individual species of *Callilepis* are plotted against the cladogram of species relationships and the *Callilepis*'s cladogram is reduced (Figs. 61, 62), a disjunct pattern becomes evident (Fig. 60). It

Glossosoma 1	EU/AS/NA(w)/-----/--/AS
Rhyacophila br. 6	EU/AS/-----/NA(e)
Myadi	NA(e)/EJ/AS
Glossosoma 2	AS/NA(w)/-----/EJ/AS
Rhyacophila sib.gr.	AS/NA(w)/-----/EU/AS
Wormaldia	EU/AS/NA(w)/NA(e)
Agapetini	NA(w)/NA(e)/EU/AS
Kybos 2	NA(w)/NA(e)/EU
Kybos 3	NA(w)/NA(e)/EU

FIGURE 63. A comparison of the linear sequential distributional patterns in nine monophyletic arthropod taxa.

is true that there are broad areas of sympatry in some taxa, for example *C. schuszteri* occurs in both Europe and Asia. This apparent sympatry may be due to dispersal at some point after the *C. schuszteri* lineage had been isolated and had evolved into a distinct species.

Now that we have studied a number of north temperate distribution patterns among several arthropod taxa, let us consider all of these patterns together.

SUMMARY OF DISTRIBUTION PATTERNS

We have now examined the distribution patterns in seven different arthropod taxa occurring in the temperate Northern Hemisphere. A total of eleven individual monophyletic lineages that have distinct, disjunct representatives in three or more north temperate areas (NA(e), NA(w); EU; AS) have been detected. Using the results of a cladistic analysis of these lineages we may arrange the individual patterns of these lineages in linear sequences and match the corresponding areas (Fig. 63).

The arrangement of the areas in linear sequences (Fig. 63) tells us that perhaps each individual lineage and sequence is a segment of a larger, more generalized pattern. The sequential arrangement of areas also brings to our attention areas not represented in a particular monophyletic lineage. But the sequencing of areas must be used in conjunction with the actual cladograms because phyletic events do not always occur in a precise sequential pattern.

Consider the cladograms for the spider genus *Callilepis* (Fig. 60) and the caddisfly tribe Agapetini (Fig. 28). The same areas (NA(e), NA(w); EU; AS) are represented in each cladogram but the relationships of the areas are different in each cladogram. In the Agapetini, the area relationships occur in a straight linear sequence: Asian forms were isolated first; European forms were isolated second; finally North American forms were isolated into eastern and western segments. In the genus *Callilepis*, area relationships do not occur in a straight linear sequence: the *Callilepis* lineage was first isolated into two major segments, Asia plus western North America and Europe plus eastern North America. Species in each of these two major segments were subsequently isolated into Asian species related to western North American species and European species related to eastern North American species. Thus, the phyletic events depicted in cladograms tell us a great deal about area relationships and must be considered when analyzing area relationships.

In all of the taxa we have examined, the phyletic events depicted in the cladograms imply that ancient populations or parts of ancient populations have become separated and have subsequently evolved into distinct taxa, the allopatric speciation model. We might now ask how these taxa became isolated. Two possibilities have been suggested to account for the isolation of individuals and/or populations: (1) dispersal across preexisting barriers (oceans, mountains, etc.) and subsequent isolation and (2) the origin of barriers (opening of the North Atlantic) that divided ancient cosmopolitan populations, i.e., vicariance. In recent years, there have been biogeographers that have advocated both dispersal and vicariance explanations. Both of these types of explanations have been proposed in this symposium to explain the distribution of plants and animals (notably, Iltis as a proponent of dispersalism and McKenna and Allen as proponents of vicariance). It is not the purpose of this paper to give an account of this debate. I can only state that in my estimation the phenomenon of dispersal obviously does occur, but the resolution of whether a distribution pattern is due to dispersal or vicariance can be ascertained only after a cladistic analysis of the taxa involved and the correlation of this cladistic analysis with the geographic history of the areas in which the taxa occur (Platnick & Nelson, 1978). Hypotheses that attribute either a dispersal or vicariance explanation to an individual pattern can be corroborated or refuted based on the analysis of additional taxa. In this paper it has been shown that the taxon/area cladograms of nine independent monophyletic lineages seem to corroborate the hypothesis that the faunas of Europe and eastern North America have shared a more recent common biota with one another than either has shared with Asia (Fig. 63).

If we assume that at least some ancient cosmopolitan populations or parts of ancient pop-

ulations were divided and isolated during the earth's history, we might ask what the events were that led to division and isolation. In the taxa we have studied we are particularly interested in possible division events affecting the landmasses that are now found in the Northern Hemisphere. The first event relevant to understanding the history of north temperate taxa was the division of the supercontinent of Pangaea into a northern landmass, Laurasia, and a southern landmass, Gondwanaland, sometime in the Cretaceous. Raven and Axelrod (1974) suggest that the last possible date for the direct interchange of taxa between North America, Europe, and Africa was about 180 million years ago (Ma). From the Cretaceous to the present, many populations have displayed considerable east-west, north-south movements throughout the history of the north temperate areas (the work of Margaret B. Davis, this symposium, gives examples of recent movements of some plant species). The older fossil record is indicative of movement and strongly indicates that elements of the north temperate biota once existed in more northern latitudes than at present. It has been suggested (Chaney, 1947; Kendeigh, 1961) that the ancestors of the present-day temperate deciduous biota existed at high latitudes in a more or less continuous band around the circumference of the Northern Hemisphere. If this is true, then these biotas have been subject to a number of distinct geological events occurring in the Northern Hemisphere.

The fossil and geological record indicates that portions of the Northern Hemisphere have been periodically inundated by epicontinental seas. Two such epicontinental seas were the Midcontinental Seaway that divided North America into eastern and western sections and the Turgai Straits that divided Europe and Asia. These seaways were active in the Upper Cretaceous (100 Ma). Cox (1974) suggested that these seas divided an ancient dinosaur fauna into distinct groups, an Asiamerica Group and an Euramerica Group. The Euramerica area was divided in the Eocene (45 Ma) by the opening of the North Atlantic (Raven & Axelrod, 1974; Cox, 1974). The Asiamerica area was first severed in the Oligocene (40 Ma) (Cox, 1974; Colbert, 1973).

Concurrent with the Midcontinental Seaway (Upper Cretaceous) was the beginning of the orogenies that gave rise to parts of the western Cordilleran mountain system (Dunbar & Waage, 1969). This western mountain building began in the early Cretaceous and continued along the eastern border of the present-day Rockies, through the Paleocene, and died out by the Eocene. These early mountains were eroded, filling the intervening basins so that by the Oligocene this western area became a flat surface 2,000 to 3,000 feet high. This peneplained, elevated area was not high enough to create an eastern rain-shadow effect. Thus, during the Oligocene the eastern and western biotas of North America were reunited as the Midcontinental Seaway subsided. The European seaway, the Turgai Straits, also subsided and the biotas of Europe and Asia were also reunited.

During the Miocene the mountain areas of western North America again became active. Uplifting occurred along the entire Cordilleran range from Alaska into Middle America (Dunbar & Waage, 1969). In addition to this mountain building, climatic changes took place throughout the world. These events eventually led to the separation, once again, of North America into eastern and western biotas and the separation of Asian and European biotas. In the intervening areas separating these continental biotas, extensive grassland biomes began to develop.

The geological history of the Bering Straits after the Oligocene is one of repeated land connections and disjunctions between Siberia and North America (Colbert, 1973). The connections have provided opportunities for plants and animals to disperse and establish cosmopolitan populations. The disjunctions would have isolated segments of these cosmopolitan populations and provided opportunities for allopatric speciation to occur.

The geological events that have just been discussed have been correlated with phyletic events in nine of the area cladograms (Fig. 64) we have studied. (*Callilepis* and one of the *Kybos* lineages will be discussed separately.) We may see that there is an orderly, sequential occurrence of both phyletic and geological events through time. The connections and disjunctions of continents and continental parts at the different time intervals can be depicted schematically (Fig. 65), illustrating how different land areas were associated.

In the diagram showing the correlation of phyletic and geological events (Fig. 64), the Miocene mountain orogeny in western North America and the worldwide climatic changes occurring at this time are shown at two points in the cladograms. The occurrence of these Miocene events is consistent with the cladograms and the geological

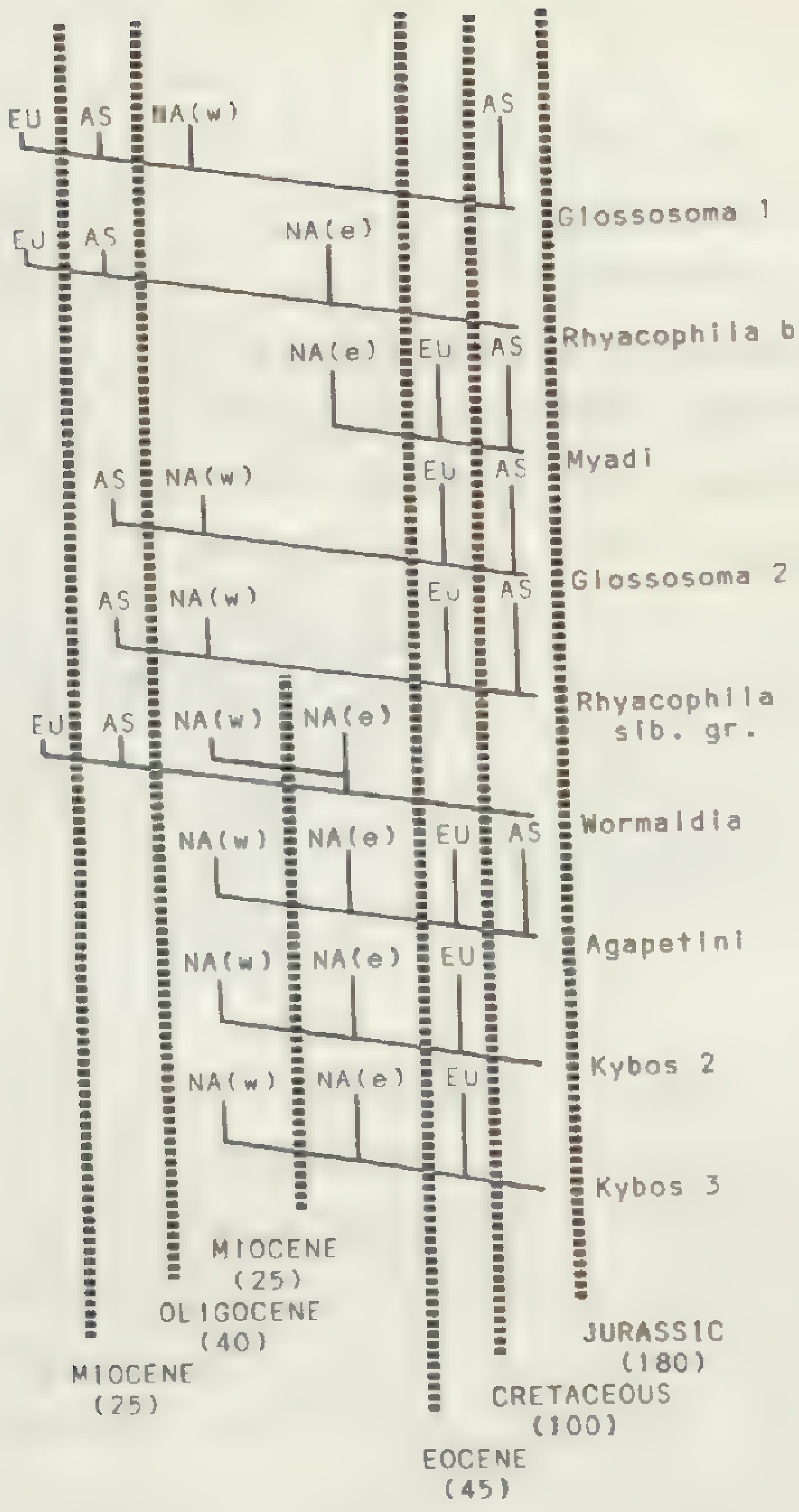


Fig. 64

FIGURE 64. The reduced area cladograms of nine monophyletic arthropod taxa superimposed on a geological time scale. It is implied that events occurring during the indicated geological periods would have divided and isolated ancient cosmopolitan populations at the points indicated on the cladograms.

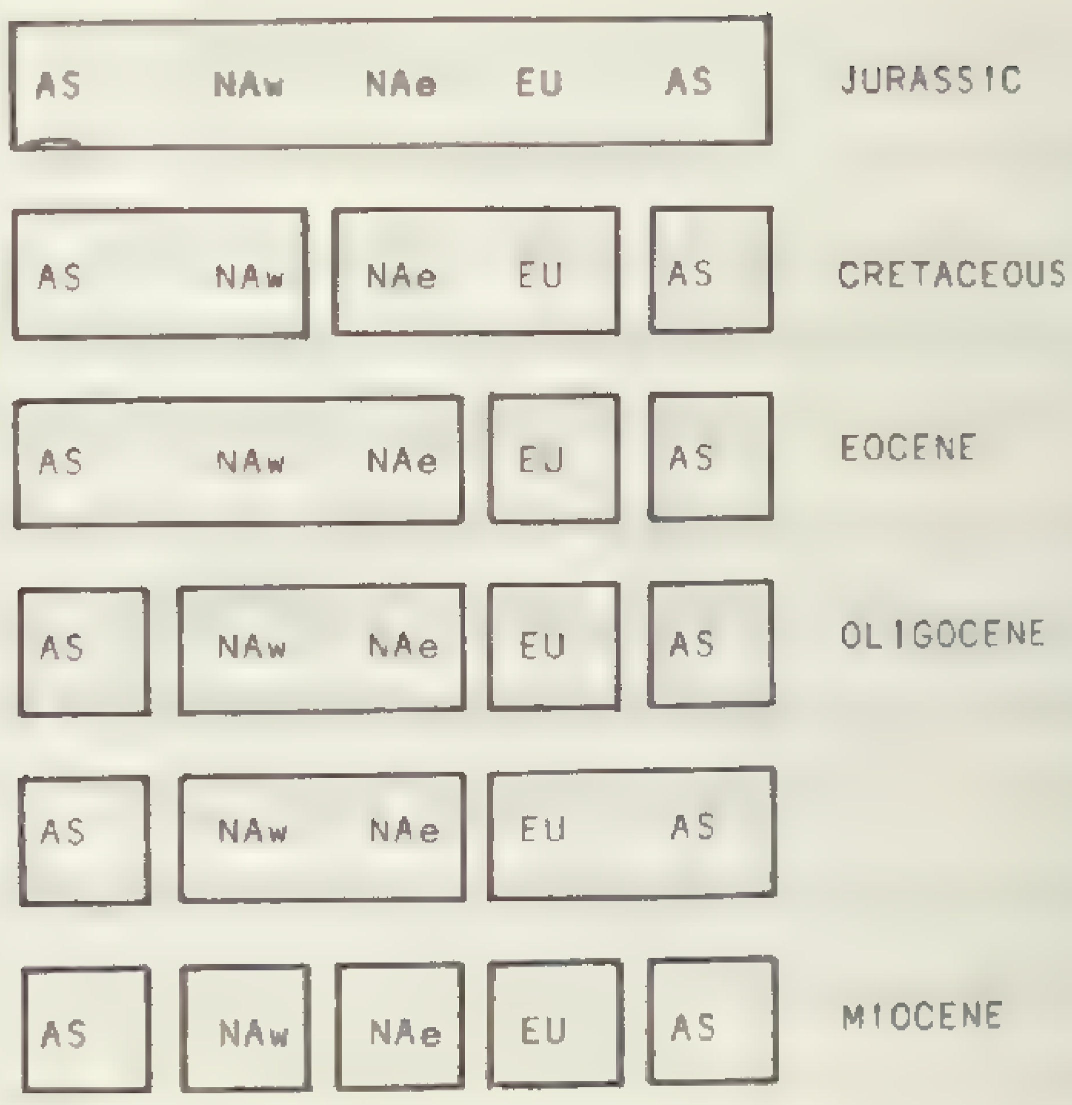


Fig. 65

FIGURE 65. A schematic diagram depicting the divisions and reassociations of North Temperate land masses during specific geological periods. These divisions and reassociations are based on information derived from cladograms illustrated in Figure 64.

history. In the two *Kybos* lineages and in the Agapetini lineage, North American populations were separated from Europe in the Eocene (45 Ma). The North American populations were subsequently divided into eastern and western segments in the Miocene (25 Ma). In these lineages (*Kybos* 1, 2, Agapetini), additional taxa have not been found in other areas. In the *Wormaldia* lineage, there was apparently a cosmopolitan population occurring in North America, Asia, and Europe. The North America and Asia-Europe connection was severed in the Oligocene (40 Ma). The now independent North American population was not divided into eastern and western lineages until the Miocene. The Asian and European cosmopolitan population of *Wormaldia* was also divided in the Miocene as were populations occurring in the *Glossosoma* 1 and *Rhyacophila* branch 6 lineages.

The *Callilepis* area cladogram is a double dichotomy (Fig. 61) that does not lend itself to inclusion with the linear cladograms of the other taxa. However, the area cladogram of the spider genus *Callilepis* may be correlated with four of the same geological events we have discussed (Fig. 60). *Callilepis* may represent a slightly different biogeographic pattern than the pattern exhibited by the other arthropod taxa we have studied. Since there appears to be a degree of sympatry among species in *Callilepis* it will be worthwhile to consider Platnick's (1976) discussion of the cladistic and biogeographic patterns of this genus in greater detail.

There are ten species in *Callilepis*. Their known distributions are indicated on the cladogram showing relationships among the ten species (Fig. 60). There are two species groups, the *nocturna* group and the *schuszteri* group. Both groups have representatives in North America, with the *nocturna* group having one species in Europe and Asia (*C. schuszteri*). At first, we might assume that a distinct pattern of population divisions (a vicariance pattern) is not evident since there are broad areas of sympatry. Platnick considered the sympatry to be dispersal "noise" and if the noise is eliminated a vicariance pattern emerges. He said, "If we assume that the presence of *C. schuszteri* in Europe is due to dispersal from Asia, the two groups of *Callilepis* can be seen as essentially vicariant on a global basis, with the *schuszteri* group occurring in southwestern North America and eastern Asia and the *nocturna* group occurring in Europe and northern and eastern North America."

Platnick next associated the two biotas, Euramerica and Asiamerica, with specific lineage divisions in the *Callilepis* cladogram (Fig. 60). These divisions correspond with the Late Cretaceous epicontinental seaways previously discussed. Fi-

nally, Platnick correlated the separation of Europe and America (45 Ma) with a separation of the *nocturna* group into European and eastern North American taxa.

The area pattern of relationships in the *butleri* lineage of the leafhopper subgenus *Kybos* (Fig. 49) is not congruent with the area patterns we have discussed thus far (Fig. 63). The *butleri* lineage indicates that a cosmopolitan population was first divided into an eastern population and a western North American-European population. Subsequently, the western North American and European population was divided. This sequence of events in the *butleri* lineage seems to represent a different biogeographic pattern. It is also possible that the cladistic relationships in the *butleri* lineage have been incorrectly determined. Whatever the case may be the *butleri* inconsistency has been noted and future workers may objectively determine the truth of the matter.

We may now conclude that of the eleven arthropod monophyletic lineages discussed only three biogeographic patterns were detected. The phyletic events depicted in the patterns were attributed to the same geological events and therefore both patterns resemble each other closely. We can say that there is a remarkable degree of congruency among the eleven cladograms. This latter statement takes on considerable more significance when the number of possible patterns that could occur are considered.

Since we only considered eleven monophyletic lineages in the summary (Figs. 63–64), the largest number of patterns we could have detected would have been eleven. We also considered only four areas (NA(e), NA(w); EU; AS). When four different areas are considered, there are two possible structurally different cladograms and 12 possible linear sequences for one of these cladogram types (Platnick & Nelson, 1978). Thus a total of 13 possible different patterns exist. The fact that only three biogeographic patterns were detected in eleven lineages indicates that individual lineages, which are members of larger biotas, have responded to historical events in a similar way. If this is true, then there may well be only a very limited number of cladistic and biogeographic patterns in nature that represent the evolutionary history of the world's biota. A great deal of work remains to be done if we are to detect and confirm the earth's evolutionary patterns. If we choose to search for these patterns using an objective, testable methodology, then this future work will lead us to a more complete and accurate understanding of the evolutionary process.

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BIOGEOGRAPHY OF OAKS IN THE ARCTO-TERTIARY PROVINCE[1]

DANIEL I. AXELROD[2]

ABSTRACT

Numerous allied trees, shrubs, and herbs inhabit the discontinuous mixed deciduous hardwood and conifer-hardwood forests of Holarctica. Their close ancestors occupied middle and high latitudes into the Middle Miocene (15–16 m.y.a.). As the forests retreated southward and were disrupted by spreading colder and drier climates following Antarctic glaciation (13 m.y.a.), numerous paired or allied species (or sections, series) originated and have survived in the disjunct segregate forests across Holarctica. In addition, all major climatic-topographic provinces served as centers of evolution from which taxa have not ranged widely. It is this latter pattern to which oaks conform most closely. Only species of allied subsects. *Prinoideae* and *Diversipiloseae* had an Holarctic occurrence, occupying lands above latitude 60°N during the late Cretaceous and Tertiary. Although climate was favorable for numerous deciduous hardwoods and conifers at high latitudes, taxa of most *Quercus* sections and subsections have been confined to one continent or to parts of them where they ranged somewhat more widely during the Tertiary. The rarity of Tertiary oaks linking Eurasia-North America may owe to the light factor (long day) at the north; fully four-fifths of all oak species occur below latitude 30–35°N and only six or seven reach latitude 50°N. Proliferation into 280 to 300 species was chiefly in response to spreading drier and colder climate that commenced in the middle Eocene, to increasing topographic diversity in the later Cenozoic, and to fluctuating Quaternary climate. At times of major climatic shifts or increased relief, oaks responded opportunistically, probably by quantum steps (punctuated equilibria) that account for the numerous series.

Oaks have left a rich fossil record in North America and Eurasia. This is expectable for the numerous species have hard, durable leaves that favor preservation, each large, spreading tree sheds thousands of leaves yearly, of which a few (or many) may contribute to an accumulating record, and they occur in many environments ranging from low to middle-high latitudes. Some 280 to 300 species are present today,[3] with their principal areas of concentration in Mexico-Central America and southeastern Asia, and with smaller areas of differentiation in the Mediterranean Basin and southcentral United States. Oaks range from the montane tropics, where evergreen taxa are prominent, to near latitude 50°N, where oaks are deciduous; *Quercus petraea* and *robur* have the most northerly distributions, reaching latitude 60°N in the Baltic region. The trees and shrubs, both evergreen to deciduous, have adapted to climates ranging from the equable montane tropics, with a twelve-month growing season, to near the borders of subalpine and boreal forests, with a growing season of three months. In terms of precipitation, they occur in most climates from perhumid montane tropical and temperate regions to the borders of deserts and in areas of very diverse seasonal distribution of precipitation. Some oaks are confined to specific edaphic conditions, as serpentine (*Q. durata*), sand barrens (*Q. incana, laevis*), limestone rocks (*Q. fusiformis*), and swamps (*Q. palustris*).

OLDER RECORDS OF FAGACEAE

Megafossils that can reasonably be assigned to the three subfamilies were in existence in the later Cretaceous. Fagoideae were then represented by *Fagus* and *Nothofagus*, Castaneoidae by *Castanea* and probably *Castanopsis* and *Lithocarpus*, and Quercoideae by *Quercus*. That Quercoideae were in existence in the Cretaceous is implied also by the occurrence of *Trigonobalanus* in the montane rain forest (elev. 1,500 m) of Colombia (A. Gentry, letter of April 1982), disjunct from Yunnan, Thailand, and Borneo; connections probably were via Africa across a narrower Atlantic on islands and old pre-Cambrian highs that have since been removed by

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[3] Although some authorities state that there are 450 oak species, C. H. Mueller (pers. comm. March, 1983) believes that 250 is more nearly an acceptable figure.

erosion (Raven & Axelrod, 1974). The megafossil and distributional data agree generally with the pollen record (Muller, 1981). Pollen of the subfamilies Castaneoideae (*Castanea, Castanopsis, Lithocarpus*) and Fagoideae (*Fagus, Nothofagus*) occur in the Cretaceous [Santonian, 80 million years ago (Ma)]. The first reliable pollen records of Quercoideae are Oligocene, probably because the grains are not especially distinctive; certainly, undoubted oak leaves are in much older rocks.

Most *Quercus* species from older Tertiary rocks can scarcely be referred to modern species, although they foreshadow them in foliar type. Members of sects. *Leucobalanus* and *Erythrobalanus* were present in the Eocene and Paleocene, and members of subsect. *Prinoideae* were also present. Oaks were already diverse in the late Eocene, as shown by nine species in the Florissant flora (MacGinitie, 1969) that reflect adaptation to subhumid climate. Fossil leaves probably assignable to subgenus *Protobalanus* (cf. *chrysolepis*) are in the Florissant flora but are not now known from older horizons. Diversity of oaks increased in the Oligocene and by the Miocene many essentially modern species were present. Records of their past distribution provide reliable clues to the Tertiary history of the genus.

Neogene Distribution Patterns in Holarctica

To evaluate the historical biogeography of oaks in the temperate forests of the Northern Hemisphere, it is appropriate to review the distribution of taxa associated with them and that still live with their descendants. Neogene floras of middle and higher latitudes are made up of species derived chiefly from mixed deciduous hardwood forests that gave way to conifer-hardwood and then to pure subalpine conifer forests in cooler regions. Many of the fossil floras occur now in areas that support sclerophyll woodland, steppe, grassland, desert, taiga, and tundra vegetation that displaced the rich temperate forests as conditions became drier and colder following the middle Miocene. The general composition of the Neogene floras reviewed here is in terms of the geographic occurrences of modern taxa allied to fossil species, with special note taken of the presence of oaks in floras that are scattered across Holarctica. It is these occurrences that clarify their history.

Numerous fossil species recorded in Neogene floras of the far West are similar to taxa now in the eastern United States (Fig. 1). These species of *Alnus, Acer, Carpinus, Carya, Diospyros, Fagus, Hamamelis, Ilex, Juglans, Liriodendron, Magnolia, Nyssa, Ostrya, Persea, Prunus, Quercus* (cf. *bicolor, borealis, coccinea, falcata, imbricaria, muhlenbergii, prinus, velutina*), *Sassafras, Taxodium,* and *Ulmus* occur at many localities. They were associated with forest trees and shrubs similar to those now in the West, distributed in *Abies, Alnus, Chamaecyparis, Cornus, Fraxinus, Gaultheria, Picea, Populus, Quercus* (*chrysolepis, kelloggii, gambelii, lobata*), *Sequoia, Tsuga, Vaccinium,* and others.

Associates of the Neogene species in the western United States (Fig. 1) also included taxa whose nearest counterparts are now in eastern Asia (Fig. 2), notably species of *Alnus, Betula, Cercidiphyllum, Exbucklandia, Ginkgo, Hydrangea, Ilex, Lindera, Paulownia, Phoebe,* and *Zelkova.*

Fossil oaks in the Neogene of the West previously reported to have Asian affinities (e.g., *Q. myrsinaefolia, Q. stenophylla*) need reexamination; most of the records certainly are not of Asian alliance. Furthermore, the absence of oaks in the Paleogene of Alaska, apart from species of subsects. *Prinoideae-Diversipiloseae,* raises a problem as to the identity of Paleogene oaks (e.g., *Q. nevadensis* Lesq.) previously suggested to have southeast Asian affinity. Actually, the nervation of *Q. nevadensis* shows it is more nearly allied to *Lithocarpus densiflorus* than to *Q. glauca,* with which it has been compared; this implies a probable late Cretaceous connection with east Asia, probably via Europe and across a narrower Atlantic. The Paleogene La Porte, Weaverville, and Goshen floras of western California and Oregon have oaks that have been compared with Mexican species, as *Q. durangensis, conzattii, magnoliaefolia,* and *xalapensis.*

In western Europe, there are fossil records of species similar to those now in the eastern United States (Fig. 3), distributed in *Acer, Berchemia, Betula, Carya, Diospyros, Fagus, Juglans, Liquidambar, Liriodendron, Magnolia, Morus, Nyssa, Ostrya, Persea, Picea, Quercus* (*prinus*), *Sabal, Sassafras, Taxodium,* and *Ulmus.* Their associates included taxa allied to those now in western Europe, distributed in *Acer, Betula, Cornus, Larix, Pinus, Populus, Quercus* (*petraea, pubescens, robur*), or in the extended Mediterranean (Tethyan) region, notably *Abies, Acer, Callitris, Carpinus, Castanea, Cedrus, Celtis, Cercis, Cornus, Fraxinus, Juglans, Parrotia, Pinus, Platanus, Ostrya, Quercus* (*castanaefolia, cerris, coccifera, ilex, libani, mirbeckii, sessiflora, suber*), and *Zelkova.*

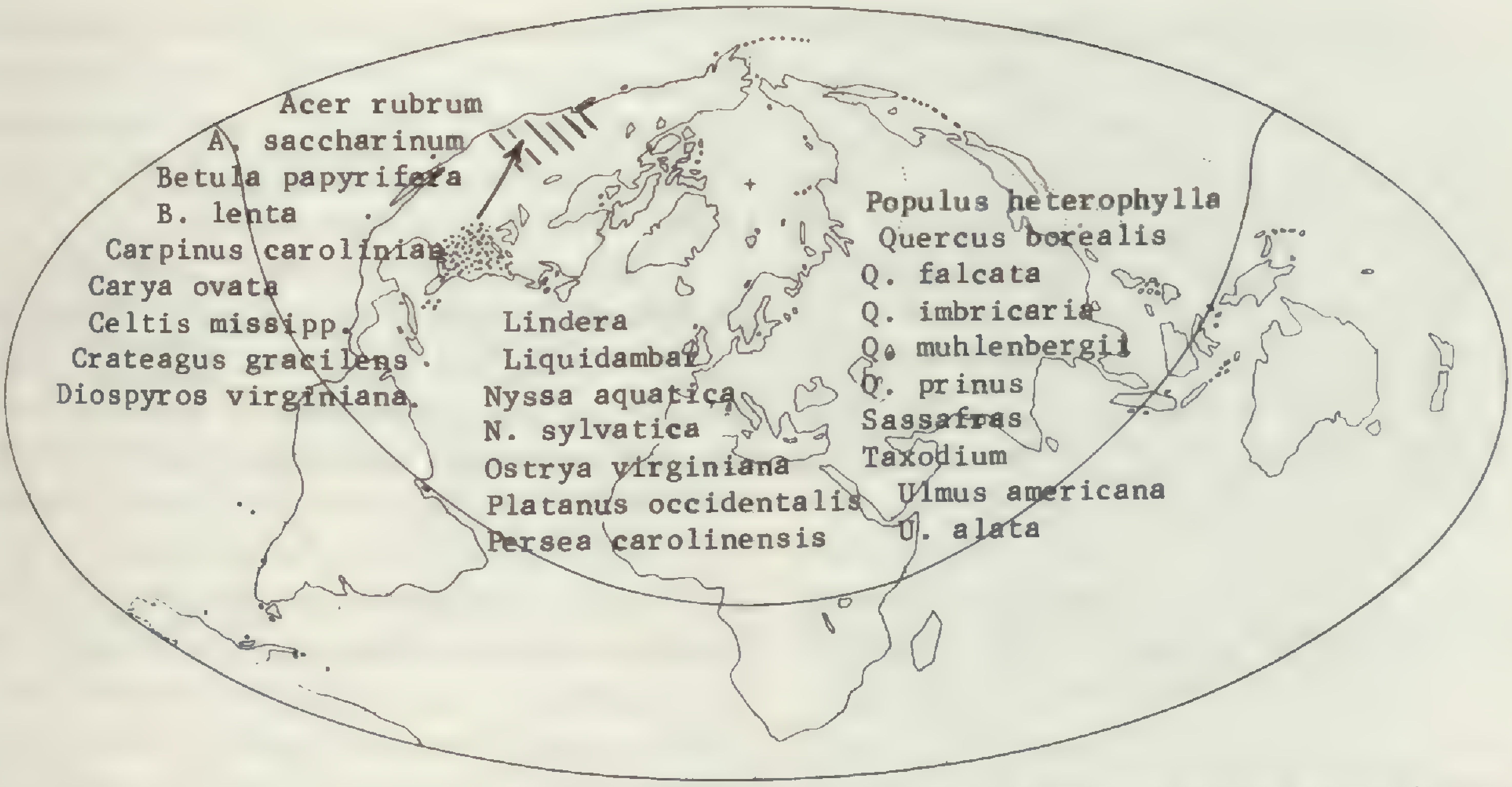

FIGURE 1. Many taxa now in eastern United States are represented by closely similar species in Neogene floras of the Far West.

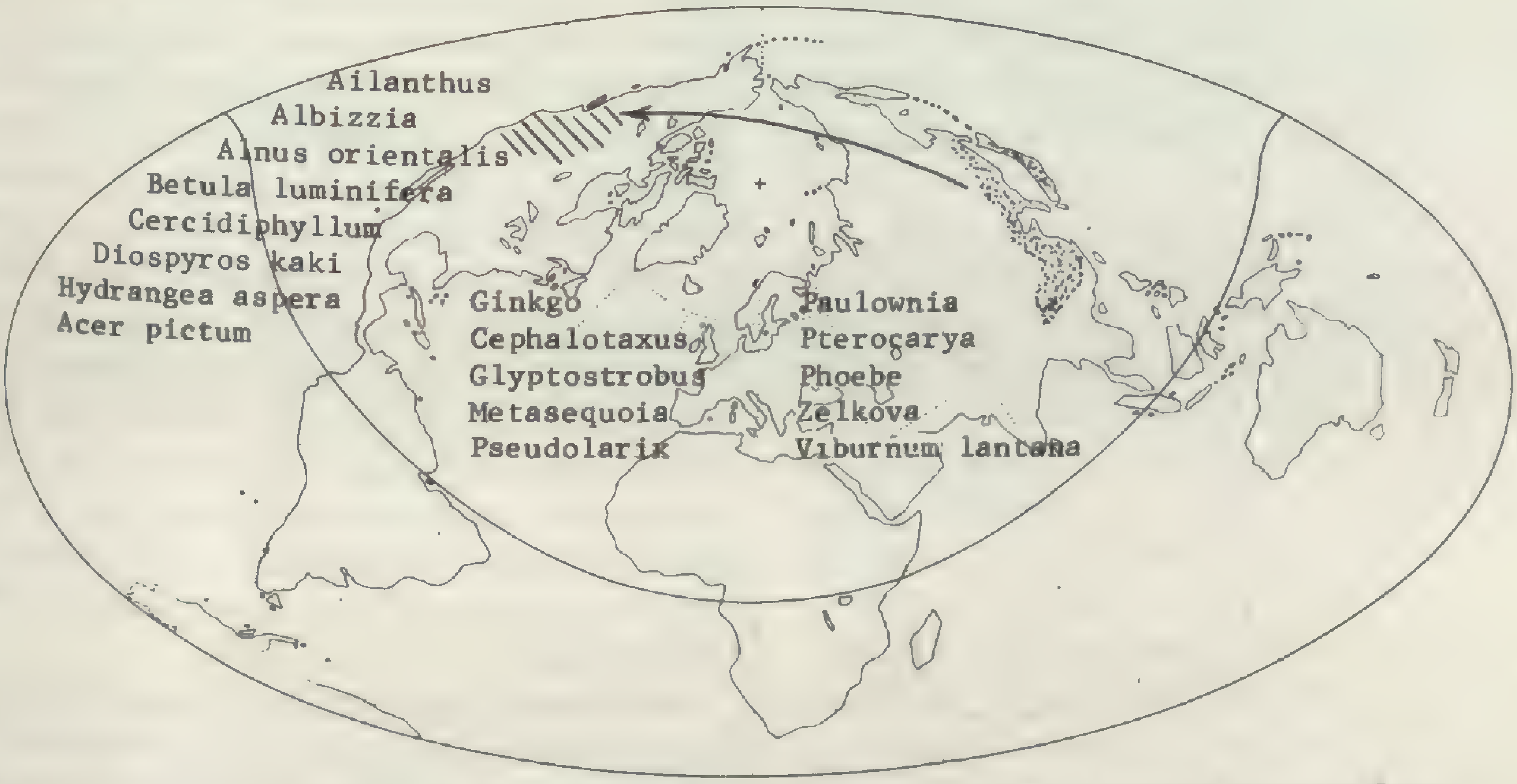

FIGURE 2. Numerous taxa now in eastern Asia have close counterparts in western Miocene floras.

FIGURE 3. Many species now in eastern United States have similar species in the Neogene of western Eurasia.

Some fossil oaks in western Europe have been compared with species now in the eastern United States (e.g., *phellos, virginiana*) or Mexico (*xalapensis*). These need restudy before they can be accepted as authentic records; judging from the illustrations, they can be matched by Eurasian taxa.

In western Europe there are also Neogene species allied to taxa now in eastern Asia (Fig. 4), including species of *Acer, Betula, Carpinus, Cathaya, Cephalotaxus, Cinnamomum, Eucommia, Fagus, Ginkgo, Glyptostrobus, Gordonia, Juglans, Larix, Liquidambar, Quercus* (cf. *serrata, variabilis*), *Sapindus, Tilia, Torreya, Wisteria,* and *Zelkova.* They were associated with fossil species related to those now in western Europe and eastern North America (Fig. 3).

There also are Neogene fossils in Japan that are allied to taxa now in the eastern United States (Fig. 5). These include species of *Acer, Betula, Carya, Carpinus, Cercis, Comptonia, Fagus, Juglans, Liriodendron, Nyssa, Platanus, Populus, Robinia, Sassafras,* and *Taxodium.* Some of the disjunct taxa are quite similar, as in *Acer* sect. *Rubra* (Fig. 6), having been derived from a common, widespread northern species [*A. trilobatum* (Sternb.) Al. Braun]. The associates of these species in eastern Asia were primarily taxa related to those now confined to that general area. Among the species of *Quercus* recorded in China-Korea-Japan are taxa allied to *Q. aliena, acutissima, dentata, gilva, glauca, mongolica, myrsinaefolia, phillyraeoides, serrata,* and *variabilis.* They are especially abundant in the Miocene floras of the region but rare to absent in older floras.

Some reports of otherwise wholly temperate American taxa in Japan probably are not valid. *Acer* sect. *Saccharina,* recorded as fossil from Washington to Nevada, is reported from samaras in Japan (i.e., *A. yoshiokensis,* Tanai & Suzuki, 1960), but they are quite similar to those figured as *A. pseudogianella*; the leaves may represent a species of *Acer* sect. *Campestre. Acer* sect. *Macrophylla,* represented only by *A. macrophyllum* of the Pacific States, has numerous fossil records in Washington, Idaho, Oregon, and Nevada. Some leaf fossils in the Neogene of Japan (i.e., *A. protodistylum* Endo) have been compared with *macrophyllum* but appear to represent a maple more nearly allied to *distylum.* Miocene lobed oaks recorded from Japan (Tanai & Yokoyama, 1975) were compared with *Q. alba* and *lyrata.* However, similar leaves from Primorye (Ablaev et al., 1974; Ablaev & Gorovoi, 1974) more probably represent sect. *Cerris* (cf. *Q. cerris* L., in Camus, 1936–38, pl. 65–66) as judged from the nature of the leaf lobes. A reported possible red oak (subsect. *Rubreae*) from Primorye (Albaev & Gorovoi, 1974) appears to be a terminal leaflet of *Acer* (cf. *negundo*).

To complete the picture, it is recalled that a number of species in the western Miocene floras from the latitude of central California-Nevada southward have their nearest allies in the subhumid woodlands that dominated the Madrean province of the southwestern United States and Mexico (Axelrod, 1958). Among these are species of *Arbutus, Bumelia, Celtis, Diospyros, Cercocarpus, Malosma, Peraphyllum, Populus, Rhus,* and *Sapindus.* Many oaks are recorded, including those allied to *Q. arizonica, brandegeei, dumosa, emoryi, mohriana,* and *oblongifolia.* The Paleogene floras in the interior include taxa similar to those in warmer, subhumid climates of Mexico and the Southwest. Xeric oaks in the Florissant flora (35 Ma) suggest alliance with *Q. brandegeei, chrysolepis, dumosa, incarnata, lobata,* and *undulata.* They formed woodlands bordering temperate mixed deciduous forest that covered moister valleys and slopes that included species allied to those now in eastern and western North America and eastern Asia (MacGinitie, 1953). The Middle Eocene Green River flora, allied largely to species contributing to vegetation now in west-central Mexico (Jalisco), has oaks comparable to *benthamii* and *polymorpha* and two others of uncertain modern affinity (MacGinitie, 1969).

As indicated in Figures 1–5, some forest taxa that occurred widely across Holarctica are allied to species now in relict or restricted areas, such as *Ginkgo* (Fig. 7), *Pseudotsuga* (Fig. 8), *Sequoia* (Fig. 9), *Liriodendron* (Fig. 10), *Juglans cinerea* (Fig. 11), *Cercidiphyllum* (Fig. 12), *Pterocarya* (Fig. 13), *Zelkova* (Fig. 14), *Eucommia* (Fig. 15), and *Ailanthus* (Fig. 16) (for others, see Tralau, 1963; Walter/Straka, 1970; Meusel et al., 1965, 1968).

Such distributions contrast with present occurrences of widely distributed allied species of diverse genera, as *Populus* (Figs. 17, 18), *Betula* (Fig. 19), *Acer* (Fig. 20), *Pinus* (Fig. 21), and many others. Some modern alliances (sections or subsections) now have more restricted distributions, such as discontinuous between the continents for *Acer* sect. *Macrantha* (Fig. 22), *Populus* sect. *Aeigeros* (Fig. 23), *Acer* sect. *Palmata* (Fig. 24), or *Acer* sect. *Rubra* (Fig. 6). By contrast, others are discontinuous on a continent, as *Acer* sect. *Saccharina* (Fig. 25). Some sections or sub-

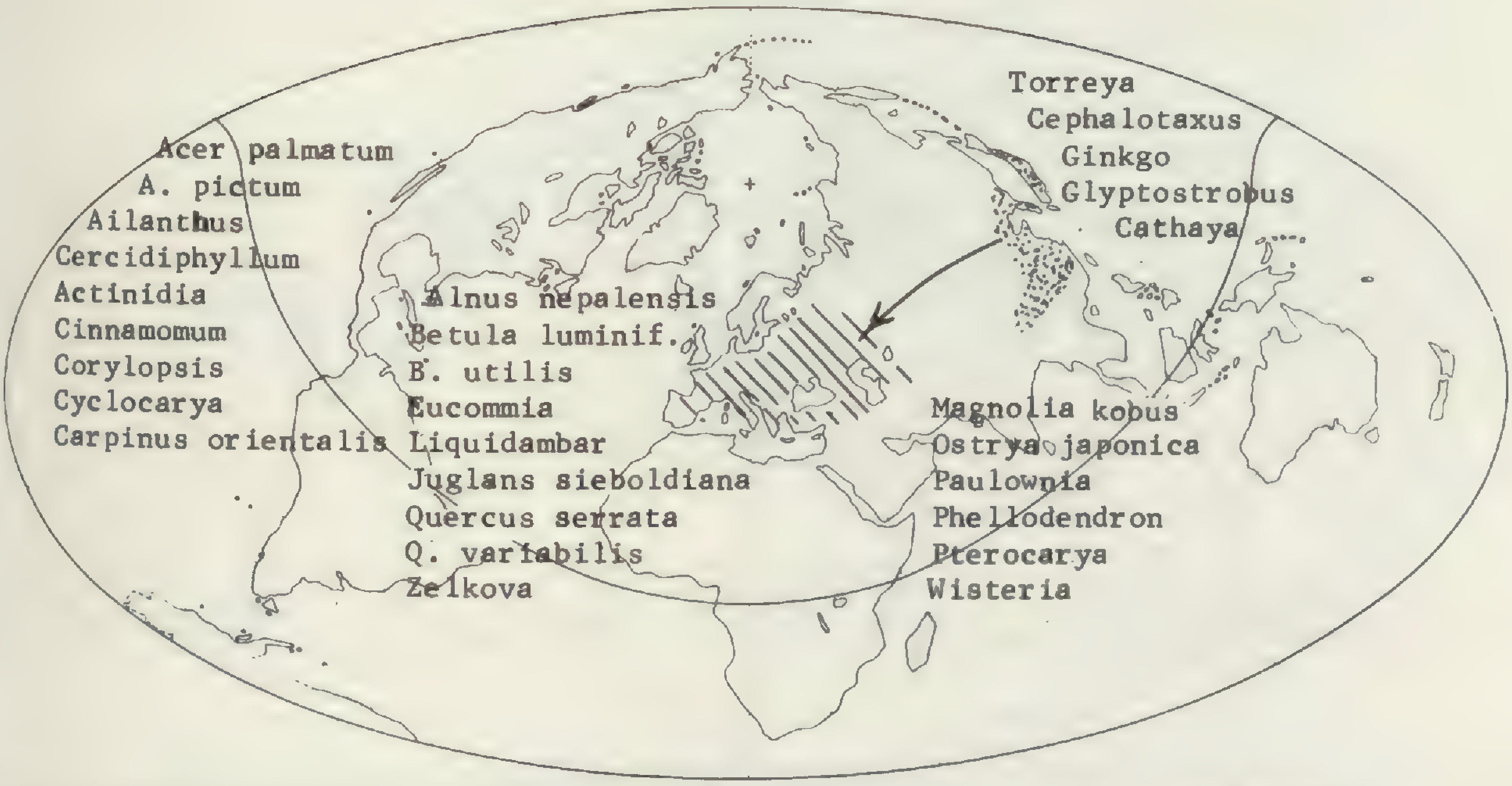

FIGURE 4. Many taxa now in the Far East occur in fossil floras of Europe and border areas.

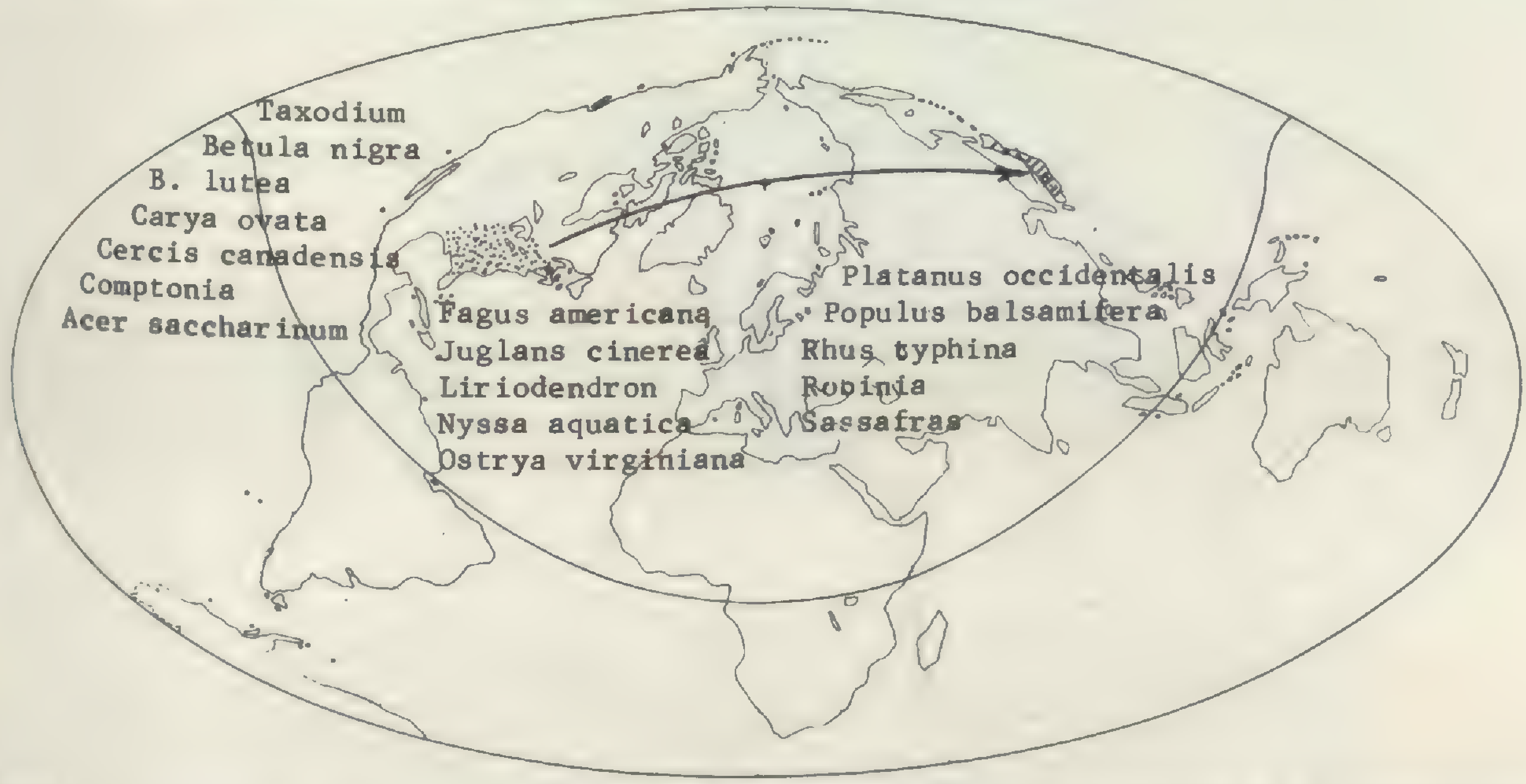

FIGURE 5. A number of species now in eastern United States have close counterparts in Neogene floras of Japan.

FIGURE 6. Disjunct maples of *Acer* sect. *Rubra* ser. *Rubra* imply a wider distribution for the ancestral taxon, a relation confirmed by the wide distribution of red maple in Eocene and later floras.

FIGURE 7. *Ginkgo*, now confined to eastcentral China (+), had a wide Holarctic distribution from the Paleocene into the Neogene as indicated by some of its fossil localities (●).

FIGURE 8. *Pseudotsuga* is widespread today in western North America but has only relictual stands (+) in eastern Asia. Fossil localities (●) indicate its wider distribution in the past.

FIGURE 9. *Sequoia*, confined now to coastal California and adjacent Oregon, had an Holarctic Tertiary distribution as indicated by some of its fossil sites (●).

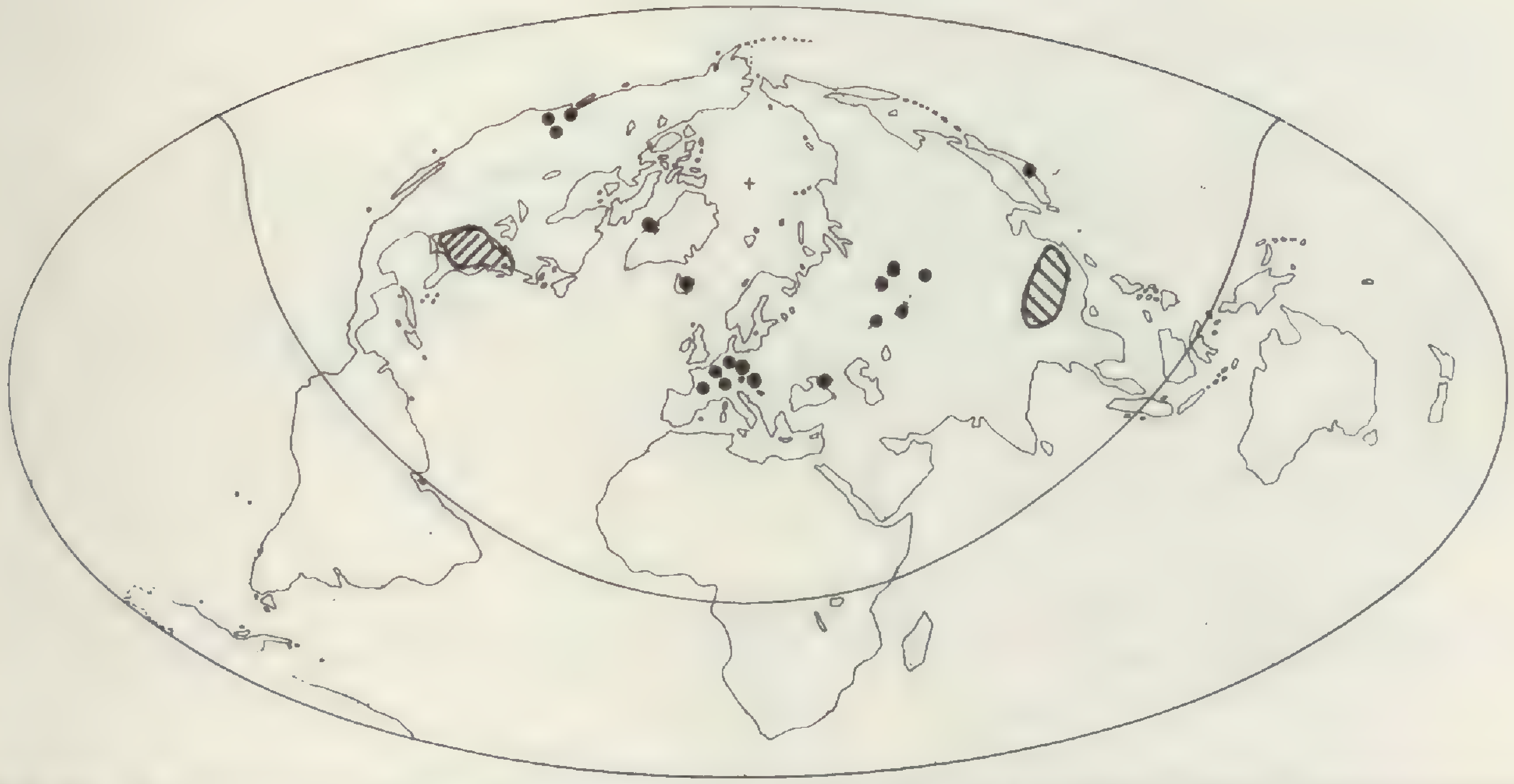

FIGURE 10. *Liriodendron* is disjunct between the eastern United States and China. Some of its fossil localities (●) shown here attest to its former Holarctic occurrence.

FIGURE 11. The distinctive fruits of butternut, *Juglans cinerea*, have been recovered at a number of Neogene sites (●) far removed from its present area in the eastern United States.

FIGURE 12. *Cercidiphyllum*, confined now to central China (+) and Japan, has been recorded at numerous sites across Holarctica, some of which are indicated (●).

FIGURE 13. *Pterocarya* species are confined now to eastern Black Sea region (+), the south shore of the Caspian Sea (+), and to central China and Japan. The fossil species (●) had a wide distribution.

FIGURE 14. Species of *Zelkova* had a wide distribution into the later Neogene (●) but are restricted now to the eastern Mediterranean-Caspian Sea region (+) and to China, Japan-Korea.

FIGURE 15. Neogene fossil localities (●) for *Eucommia*, a relictual genus confined now to central China.

FIGURE 16. *Ailanthus,* now native to China, has been recovered at a number of Neogene sites (●).

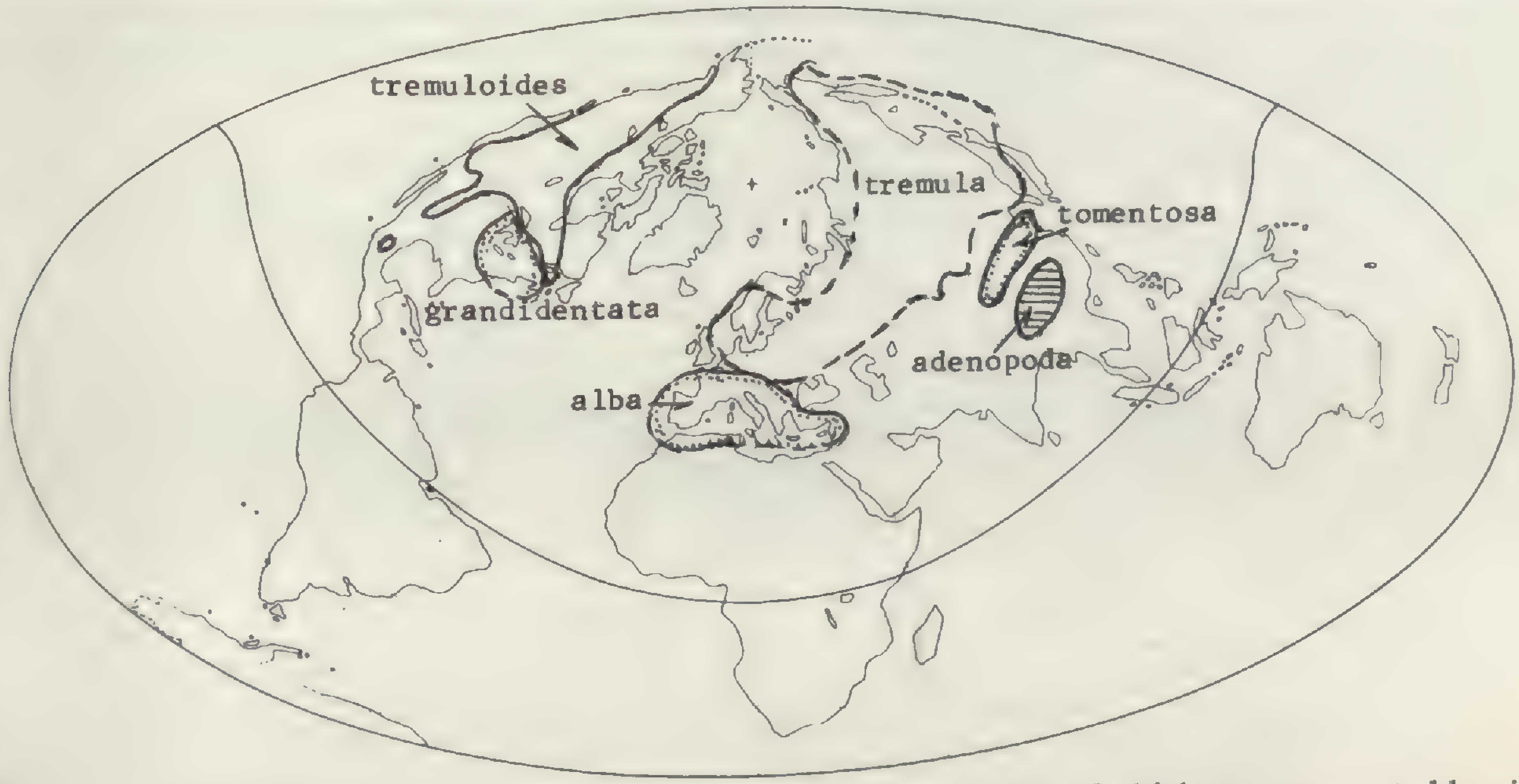

FIGURE 17. Distribution of modern species of *Populus* sect. *Leuce,* most of which are represented by similar taxa in Miocene floras of Asia and North America. The fossil record suggests that these diverged from an ancestral taxon in the Eocene, or possibly earlier.

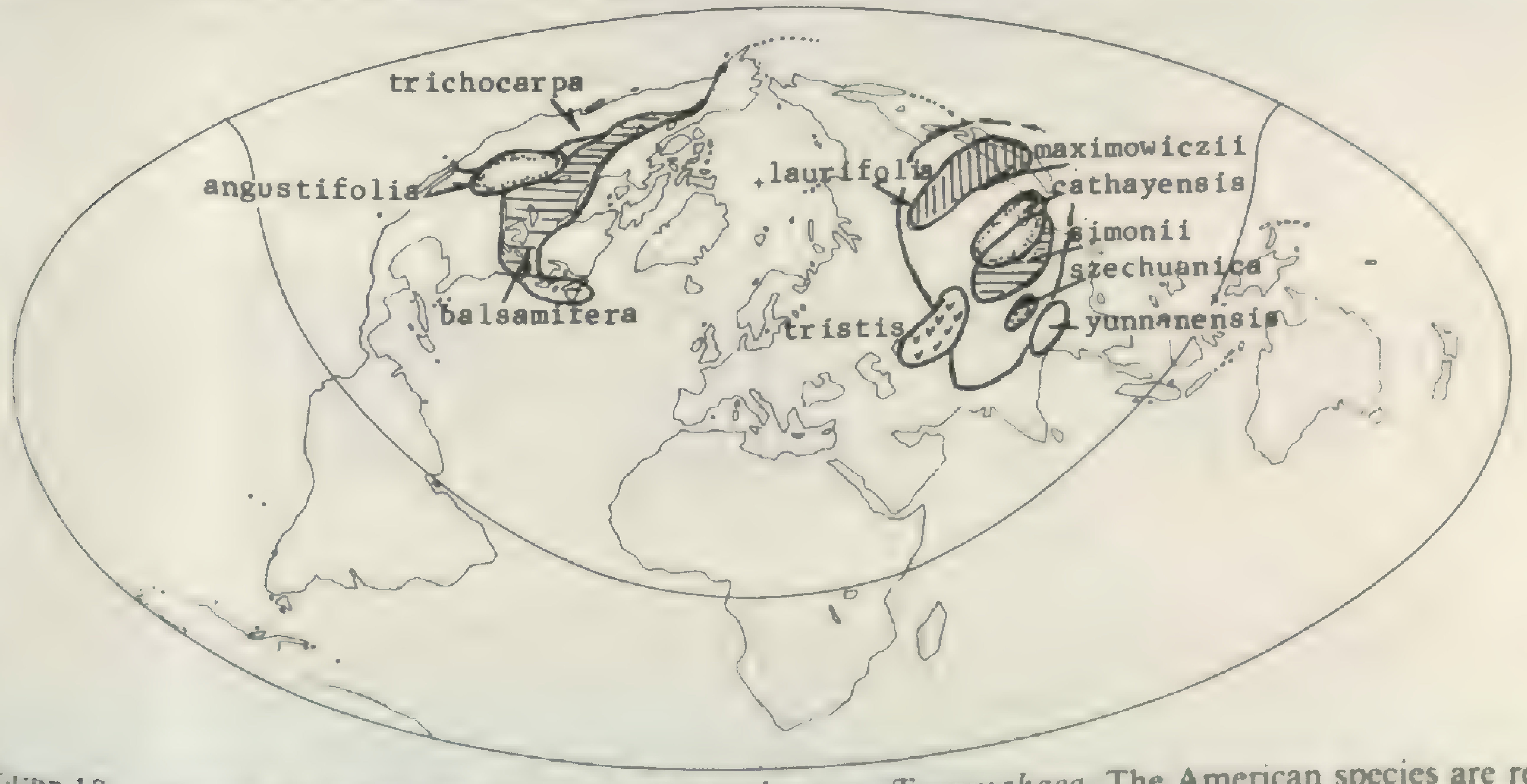

FIGURE 18. General distribution of species of *Populus* sect. *Tacamahaca.* The American species are represented by similar fossils over a wide area in western North America. Asian poplars of this group are not now certainly known from North America.

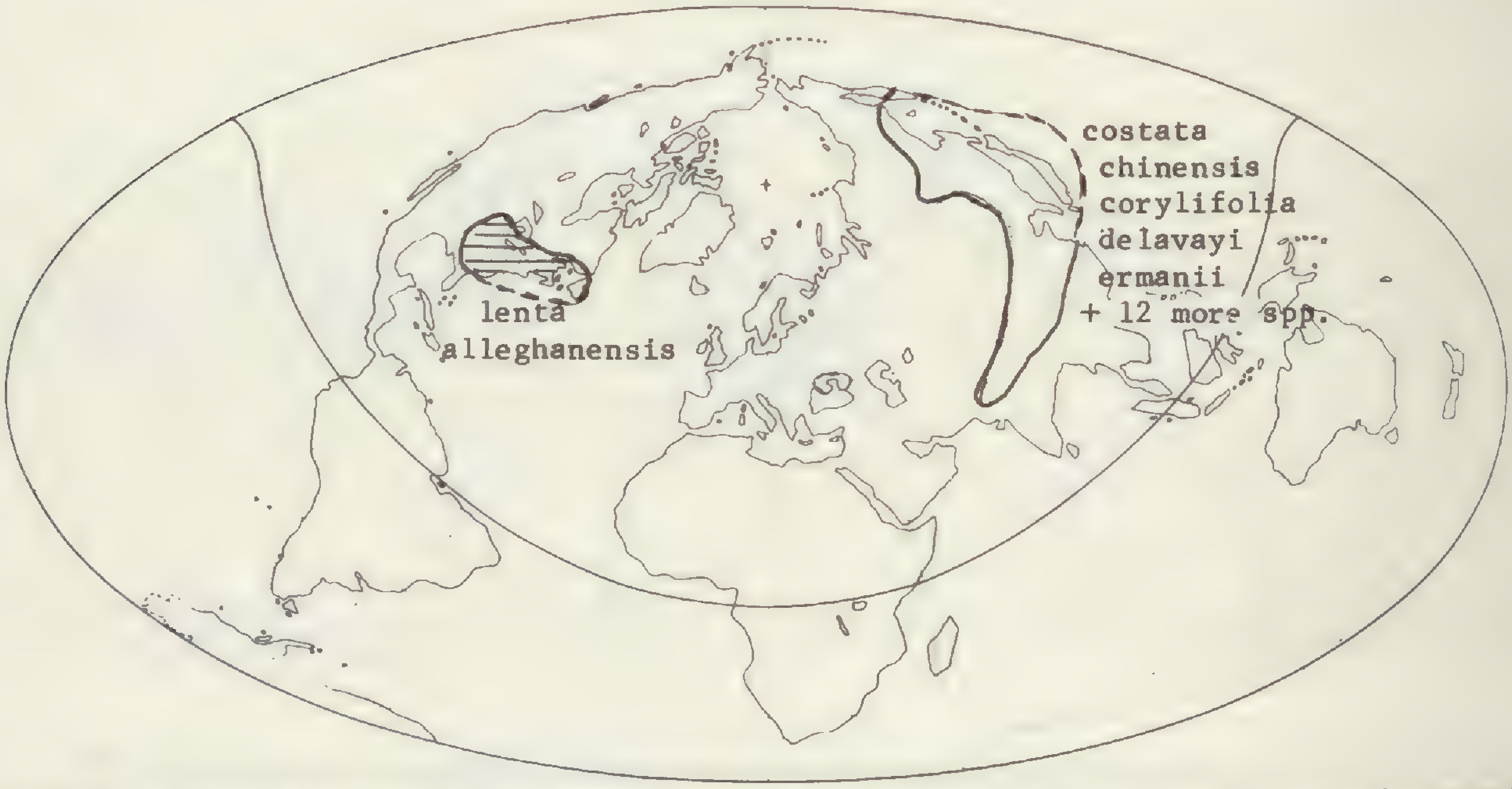

FIGURE 19. Modern species of *Betula* sect. *Costatae* are disjunct in Holarctica. Asian species are not now definitely known from western United States. The numerous species in eastern Asia imply evolution in that general area.

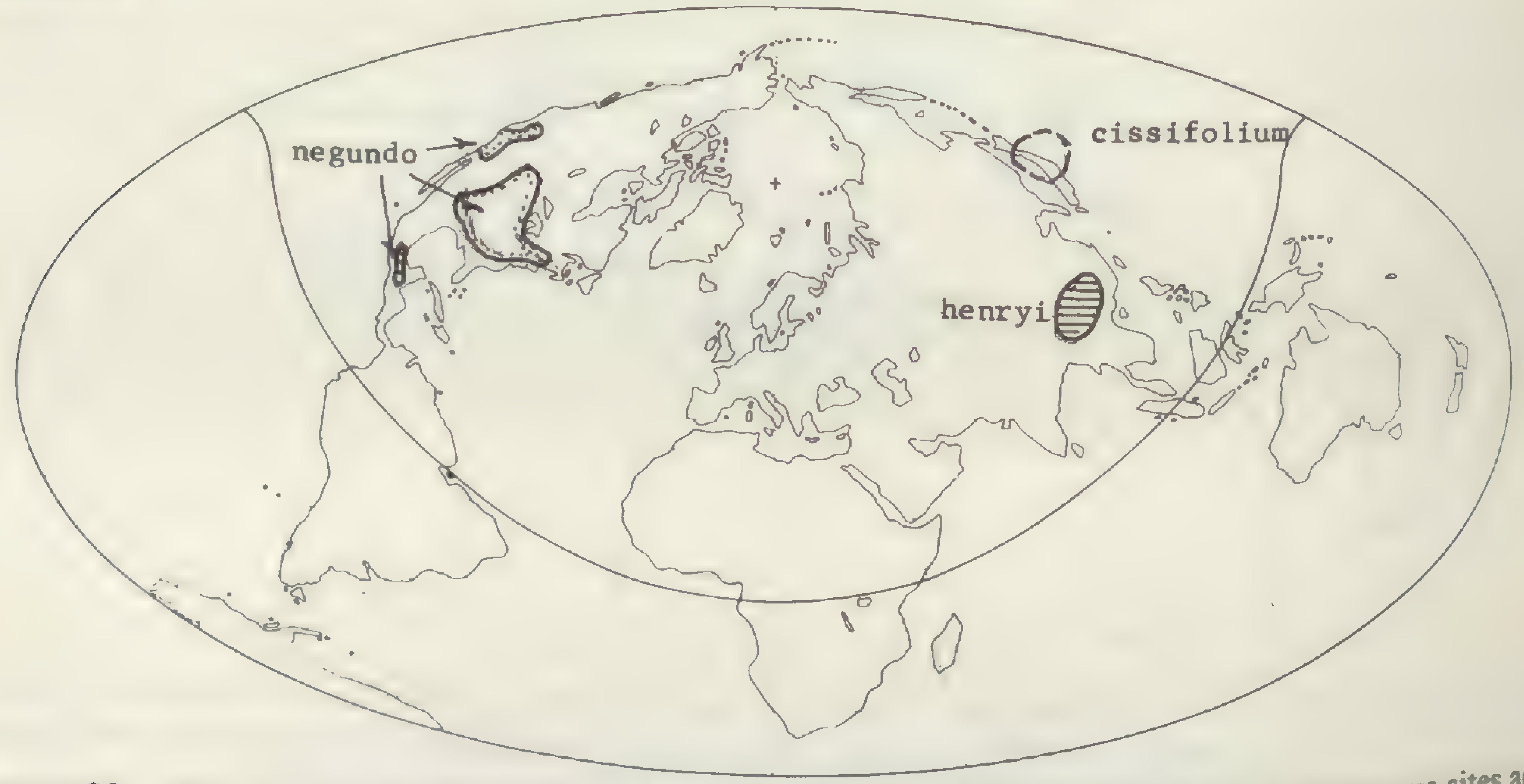

FIGURE 20. Taxa of *Acer* sect. *Negundo* are now widely disjunct but formerly lived at numerous sites across the region. Species of the alliance are recorded from the Eocene.

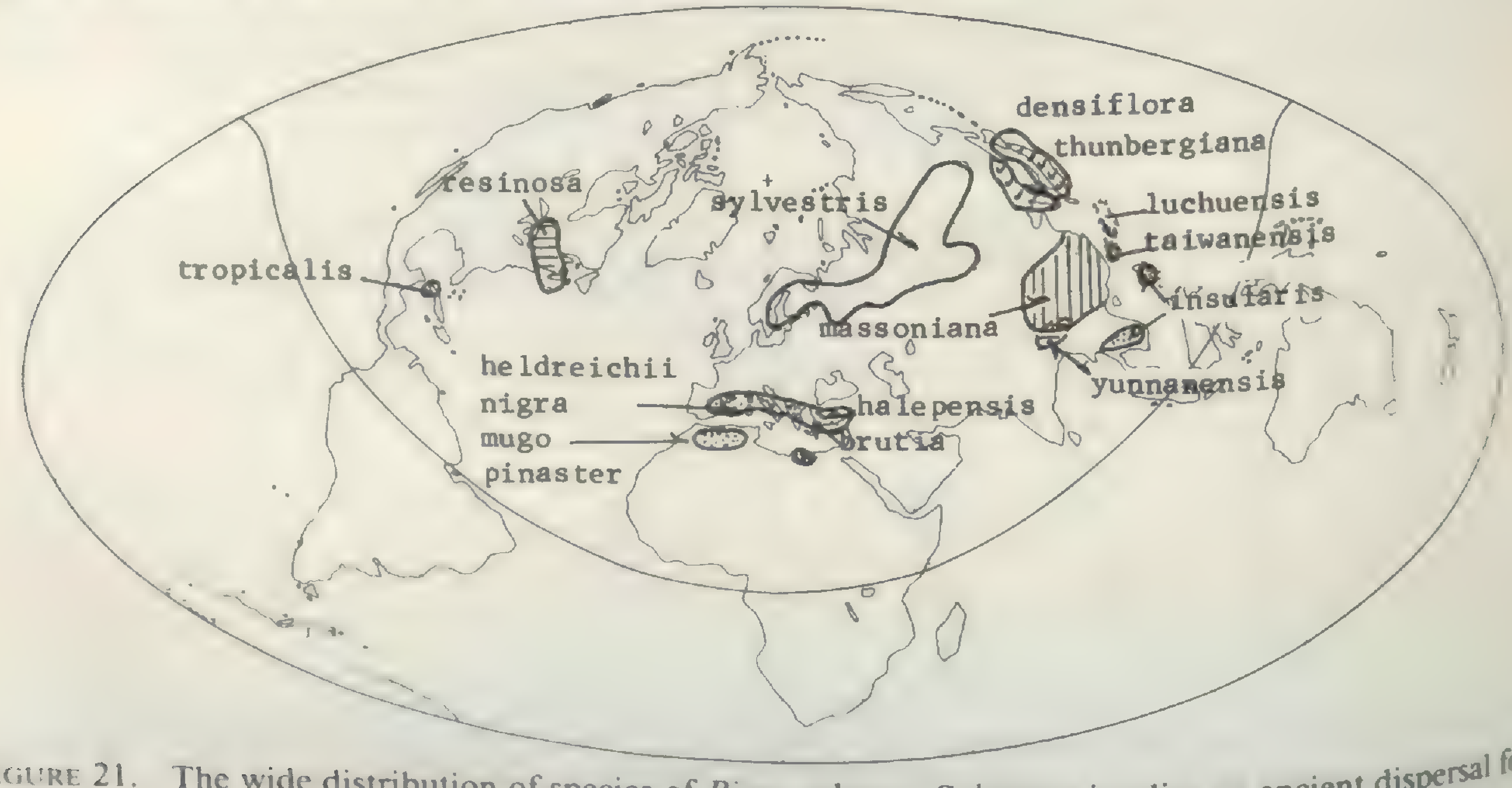

FIGURE 21. The wide distribution of species of *Pinus* subsect. *Sylvestres* implies an ancient dispersal for an ancestral group, probably in the Late Cretaceous.

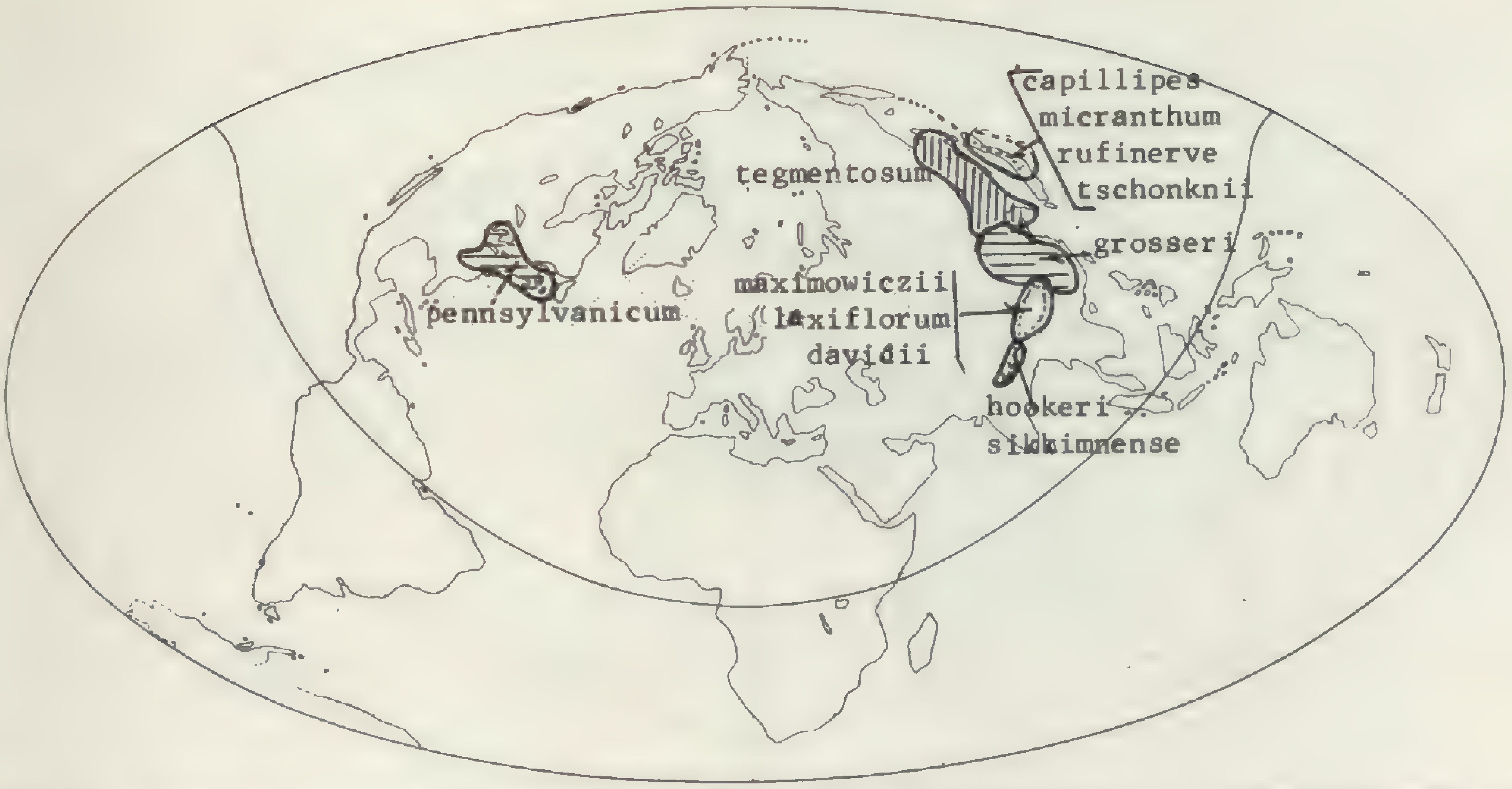

FIGURE 22. Species of *Acer* sect. *Macrantha* ser. *Macrantha* are concentrated in eastern Asia, with a single species in eastern North America. East Asian maples of this alliance are not presently known from western North America.

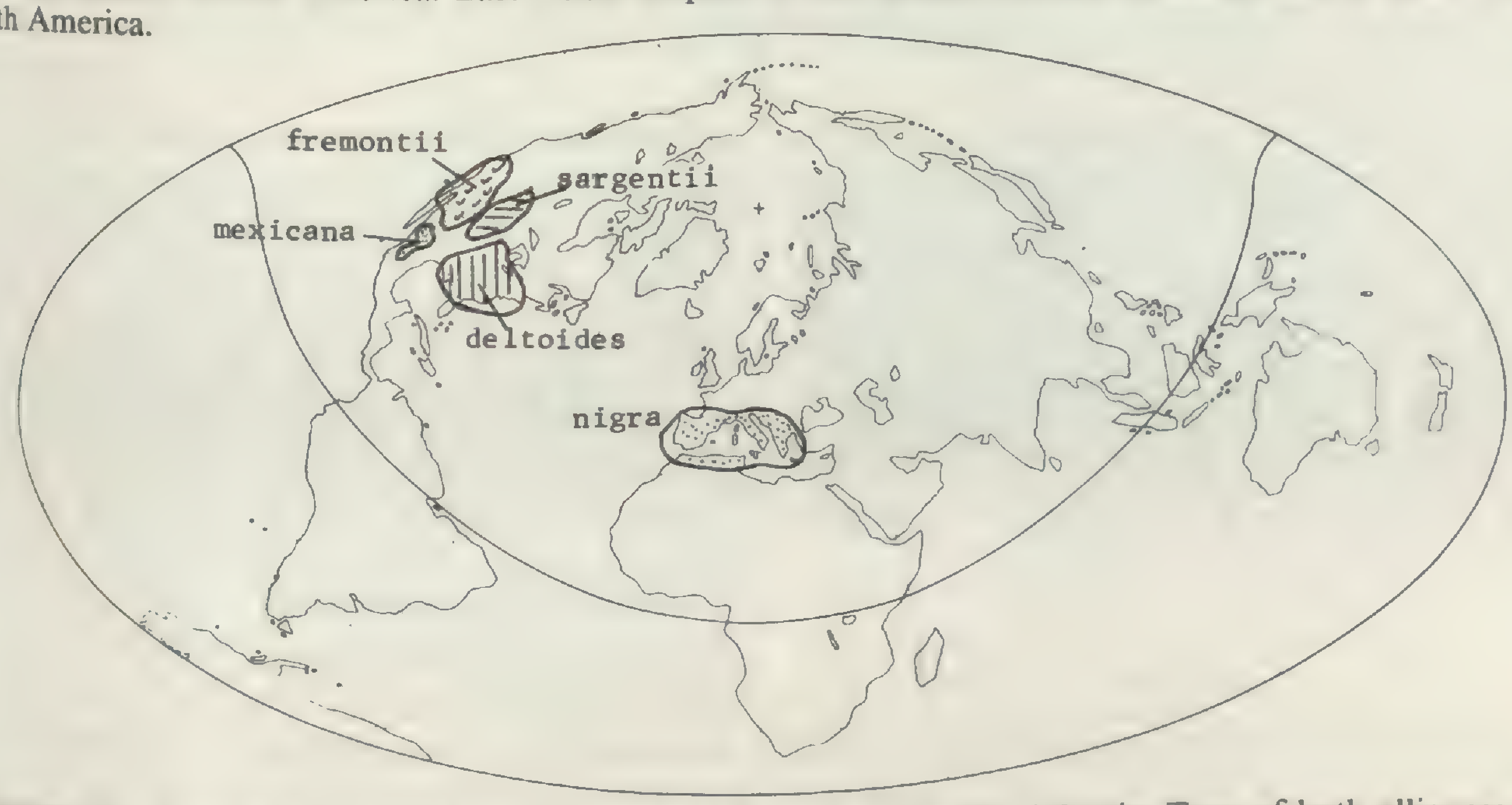

FIGURE 23. Species of *Populus* sect. *Aigeros* are disjunct across the Atlantic. Taxa of both alliances have been recorded as fossil in their respective regions and some have ranged more widely, as fossil species allied to *P. mexicana*. Trans-Atlantic connections are implied.

FIGURE 24. Species of *Acer* sect. *Palmata* ser. *Palmata* are concentrated in eastern Asia, with one along the Pacific Coast of North America. A species of this series occurs in the Eocene of Nevada.

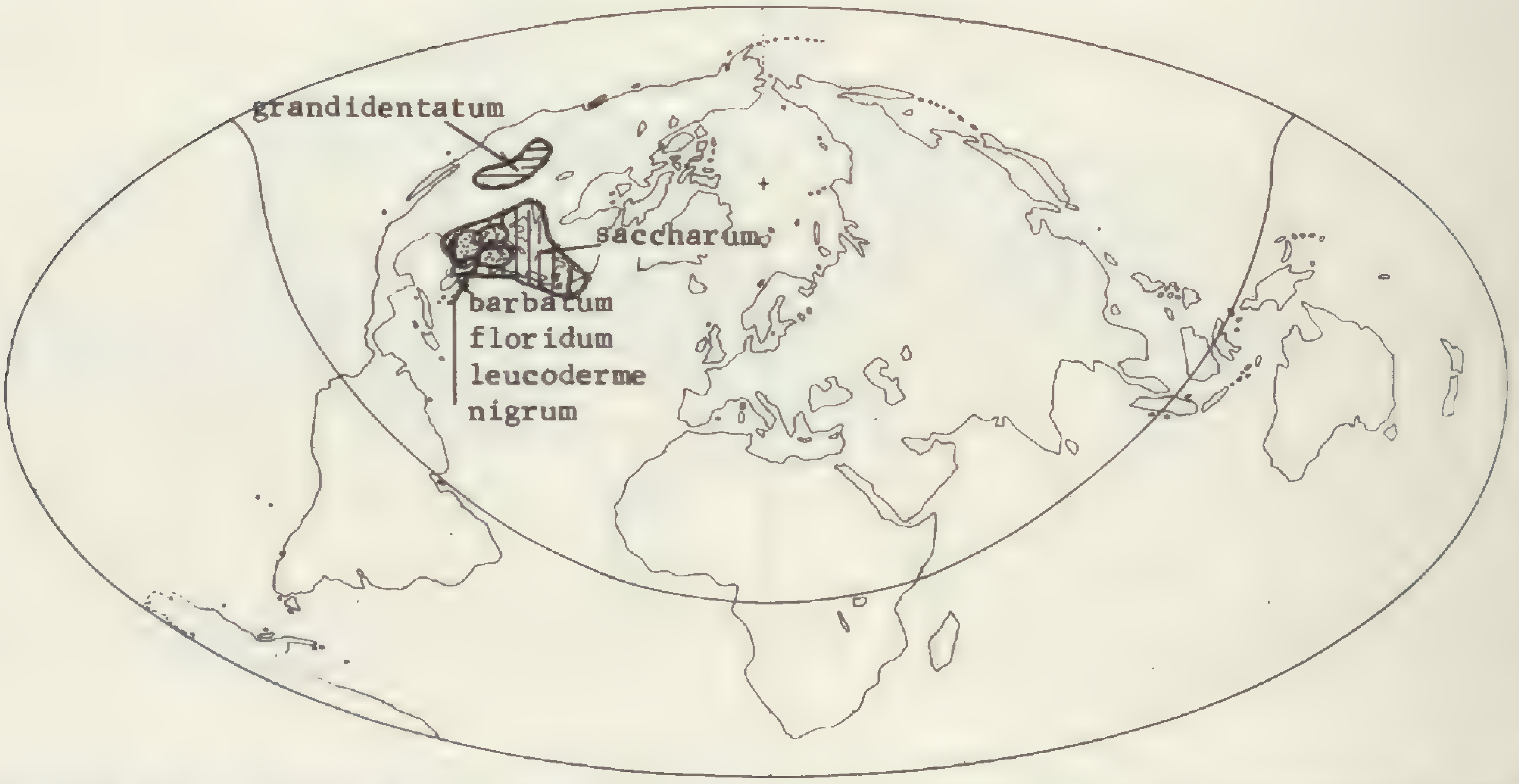

FIGURE 25. *Acer* sect. *Saccharina* is represented by disjunct taxa now in the Cordilleran region and eastern North America. Fossil species allied to *saccharum* and *grandidentatum* had a wider distribution in the far West into the Miocene.

sections are localized, as *Pinus* subsect. *Australes* (Fig. 26), *Acer* sect. *Campestris* (Fig. 27), *Pinus* subsect. *Ponderosae* (Fig. 28), as well as others such as *Pinus* subsect. *Cembroides* and *Acer* sect. *Glabra* of western North America. The fossil record shows that these (and other) alliances are represented by similar taxa in the same general region as their present areas: they have not ranged widely and seem to be in regions that represent their centers of origin.

DISCUSSION

The allied taxa in these disjunct areas of Holarctica represent the derived, broken links that contributed to the temperate Arcto-Tertiary forests into the Miocene. As emphasized earlier (Axelrod, 1959: 261–269), each region had its own unique taxa, those typical of the western United States, the eastern United States, western Europe, and eastern Asia, and they are not recorded far from their present areas: this is especially true of the oaks (see below). A similar statement applies to the Madrean and Tethyan floristic regions, characterized by numerous subhumid and semiarid autochthonous taxa that interfingered with temperate forests to the north and subtropical ones to the south. In each of these regions where ancestral taxa ranged more widely, grasslands and deserts have arisen more

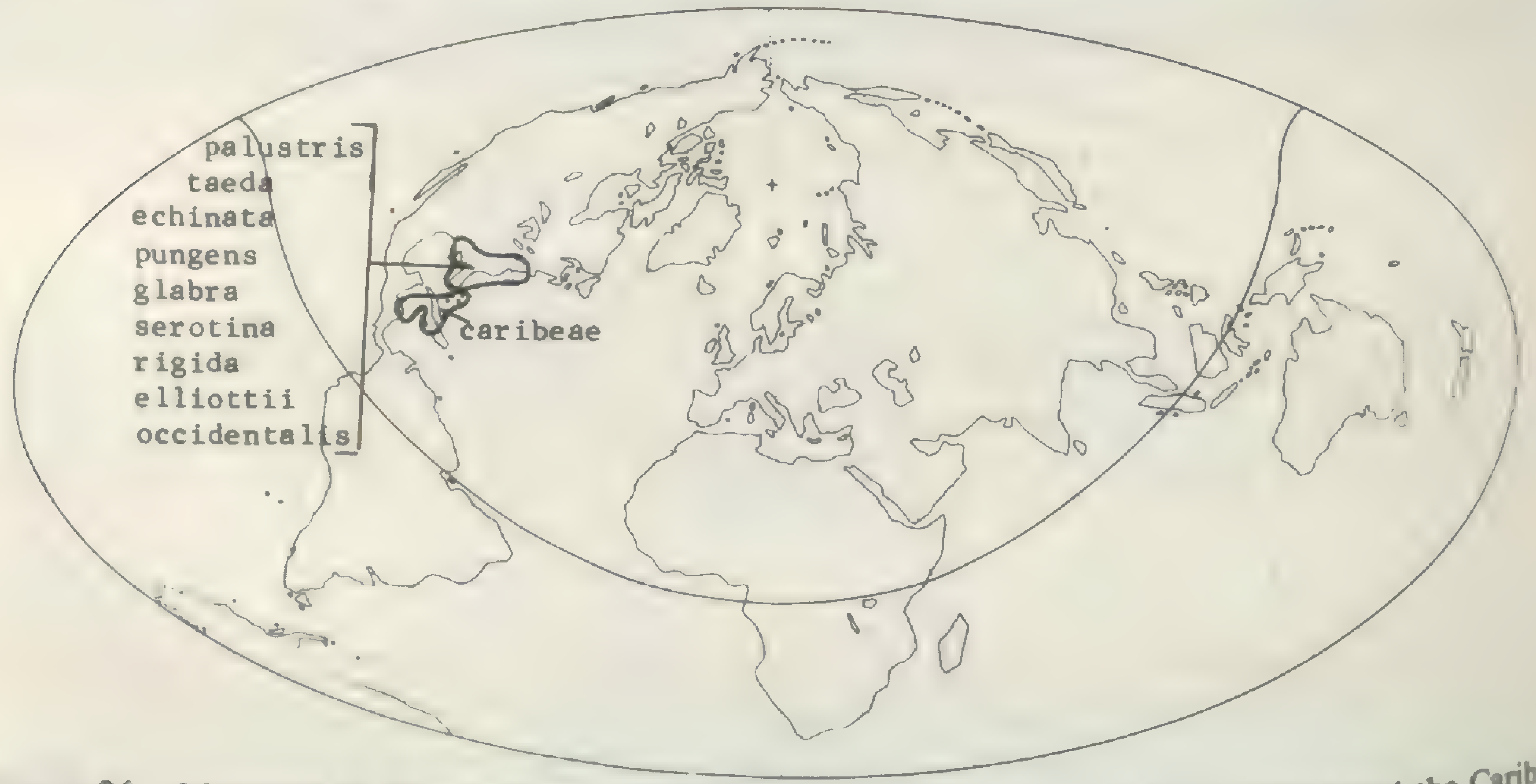

FIGURE 26. Members of *Pinus* subsect. *Australes* are confined to eastern United States and the Caribbean Islands. Some fossil pines in western Europe resemble this group.

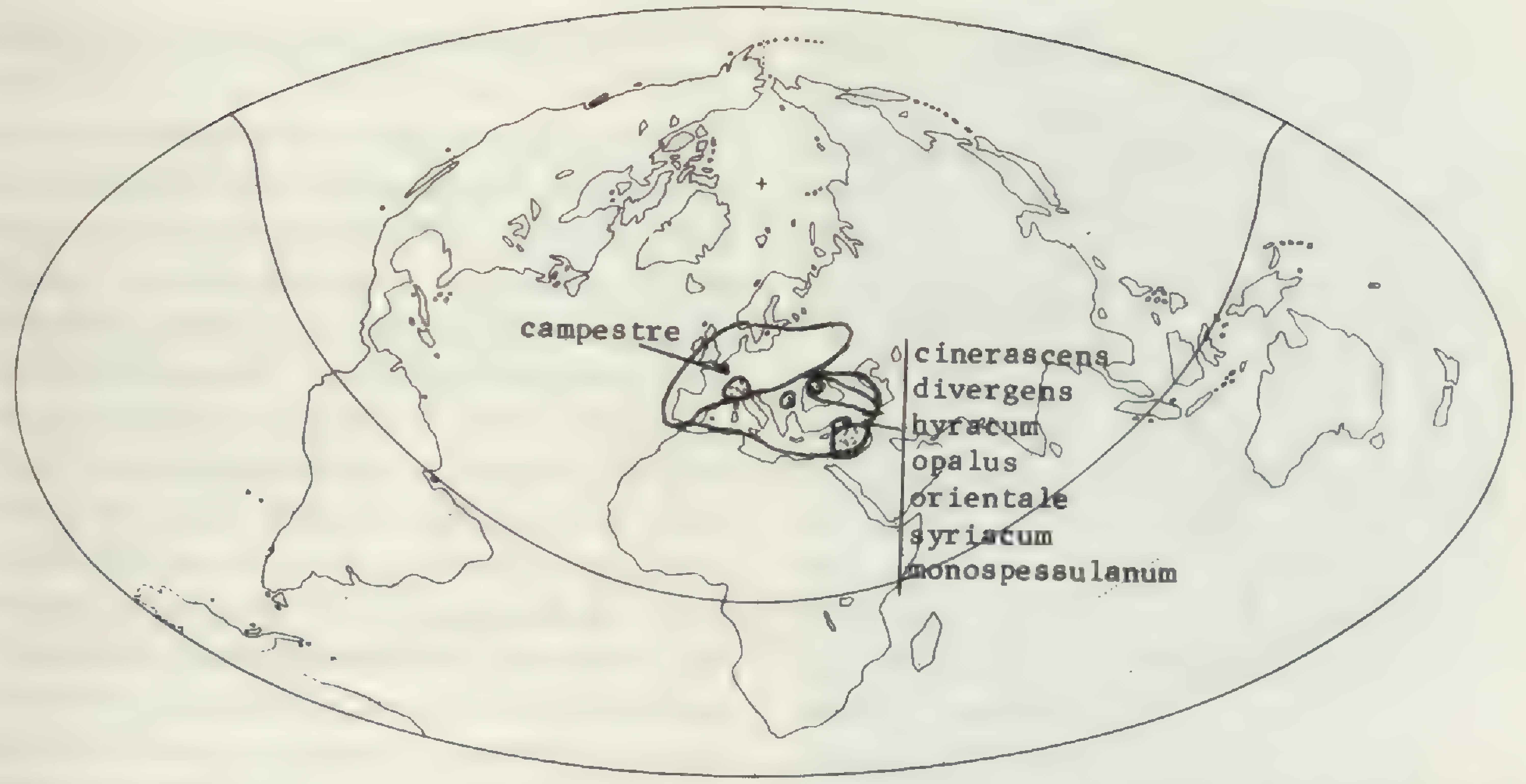

FIGURE 27. Members of *Acer* sect. *Campestris* are confined chiefly to the Mediterranean basin apart from *A. campestre*, which ranges more widely. Fossil species of this alliance are common in the area of their present occurrence.

recently to disrupt their former distribution across middle latitudes, and colder taiga and tundra climates have disrupted their occurrence at higher latitudes. Their past continuity is demonstrated not only by fossil records scattered across Holarctica, it has been inferred also from the nature of the taxa in the surviving relict forests in the Colchic region (Balkans-eastern Turkey-Caucasus), the Elbruz Mountains, the Himalayan axis, the forests of east-central China, Japan, and those of the eastern and western United States. All these disjunct areas have allied taxa in numerous genera (see Meusel et al., 1965, 1968), including sensitive mesic forest herbs that still link the widely separated relict forests that were isolated by spreading drought and cold over middle and higher latitudes following 13 Ma (Axelrod & Raven, 1972: 227; Axelrod, 1979).

The associated herbaceous understory of the mixed forest is largely unknown in the fossil record, apart from a few seed floras in western Europe, Siberia, and Japan. The former do contain

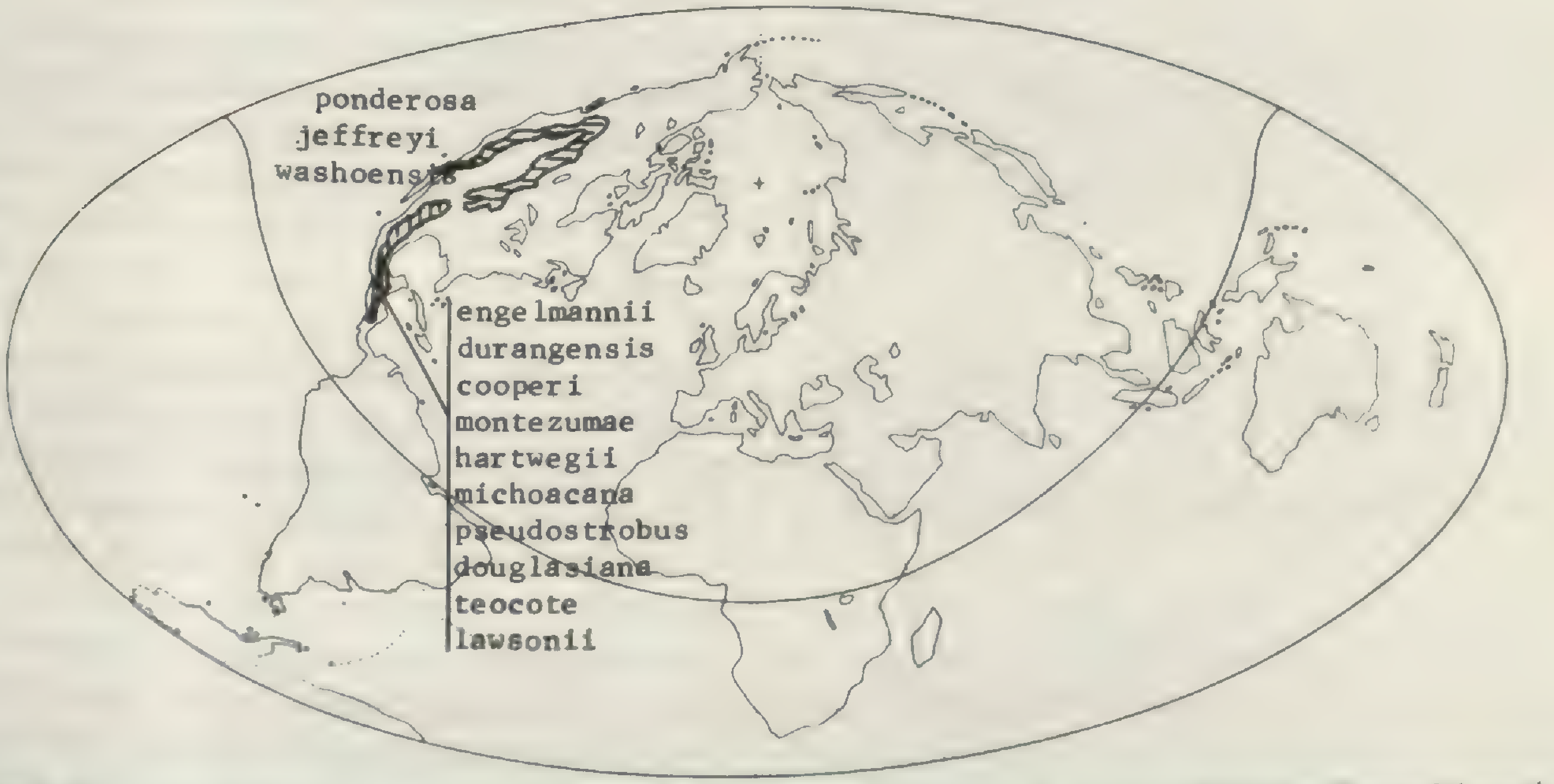

FIGURE 28. Species of *Pinus* subsect. *Ponderosae* have proliferated in the uplands of Mexico-Central America, presumably their "center of origin." Fossil pines allied to the group are recorded widely in the western United States commencing in the Oligocene.

taxa now in eastern Asia and eastern North America (reviewed in Leopold, 1967, 1969). The related herbaceous forest species now on separate continents are in *Actaea, Anemone, Asarum, Carex, Circaea, Dentaria, Erythronium, Galium, Geranium, Impatiens, Luzula, Panicum, Oxalis, Poa, Ranunculus, Senecio, Thalictrum, Sanicula, Veratrum, Viola, Waldsteinia,* and many others (see Kornas, 1972; Meusel et al., 1965, 1968). As might be expected, there are more bi-continental species between Europe and Asia than North America (Meusel, 1968, 1969; Meusel & Schubert, 1971). The European species are especially rich in the Colchic forests, and in Asia they are in relict deciduous forests of the Caucasus, Elbruz, and Himalayas and in the scattered higher mountains of arid central Asia that link the European and east Asiatic centers. The present arid central Asian region supported broadleaved mixed deciduous forests into the middle Miocene (reviewed in Axelrod, 1979). Stebbins noted that there are similar herbaceous groups confined to eastern Asia and eastern America, not only in families regarded as generally "primitive" (Berberidaceae, Liliaceae, Ranunculaceae) but in advanced families (Orchidaceae, Poaceae, Polygonaceae). The disjunct species, as in *Antenoron* (= *Tovara*), *Brachyelytrum, Cypripedium,* and *Polygonum,* are scarcely different and at most are only varietally or subspecifically distinct; these herbs are not only ancient, they have changed but little over the past 15 million years. Clearly, "the evolution of herbaceous elements (in the mixed deciduous forests) has been as slow as that of the woody species" (Stebbins, 1947: 152).

Comparison of species in the derived (segregated), temperate mixed-deciduous forests of North America, Europe, and Eastern Asia shows that many of the allied taxa (paired species, allied sections, series) have similar ecologic occurrences, occupying comparable habitats in analogous (segregate) plant communities. Their similar phyto-sociological relationships imply that their ecologic tolerances have not changed greatly since the middle Miocene (15 Ma), a time when continuous mixed deciduous and conifer-hardwood forests still linked Asia-North America (via Beringia) and Europe-North America (via Iceland-Greenland). Clearly, the North American and Eurasian paired-taxa are descendants of common ancestral forms that contributed to the Arcto-Tertiary forests (Medwecka-Kornas, 1961; Kornas, 1972).

BEARING ON ARCTO-TERTIARY CONCEPT

The preceding data, as well as those presented in Figures 1–28, certainly demonstrate the former continuity of a rich temperate forest flora across northern to central Holarctica. It was first termed an "Arcto-Tertiary element" and then formalized into the Arcto-Tertiary Geoflora (reviewed in Wolfe, 1977). Recorded in the Paleocene to Eocene of Spitzbergen, Greenland, Siberia, Ellsemereland, and northern Canada, by the middle and late Eocene temperate forest woody taxa ancestral to modern species had already occupied mountains in the central Cordilleran region (Challis and Salmon floras, Idaho; Yellowstone flora, Montana; Bull Run, Copper Basin, Elko floras, Nevada). As climate progressively cooled following the late Eocene, evolving taxa in the temperate forest flora shifted into lowland basins, first in the interior and then the coastal strip. By the Miocene many woody taxa were scarcely separable from living species.

Reports of the demise of the Arcto-Tertiary Geoflora "have been greatly exaggerated." The basis for that belief stems partly from the description of a late Middle and Upper Eocene tropical flora from coastal Alaska (Wolfe, 1972, 1977), which was then at a latitude near 70°N (Smith et al., 1981). It has been evident to me for a decade (unpubl. manuscript) that the flora, which occurs in the marine Kushtaka Formation, is allochthonous. This agrees with the fact that later Eocene floras from middle and high latitudes in Eurasia and North America regularly contain temperate forest taxa. Furthermore, geologic evidence (Cowan, 1982) indicates that part of coastal southeast Alaska (Baranof Island) was displaced northward fully 1,000 km from southern Vancouver Island since the late Eocene; other coastal terranes (i.e., Kodiak Islands) are also allochthonous (Grantz et al., 1982; Plumley et al., 1982; Hamilton, 1983). An allochthonous origin also disposes of the geophysical problem that an Eocene tropical flora and climate in a stable, coastal Alaska presents, notably one in which "the axis of rotation of the earth may have had a much less—possibly no—inclination" (Wolfe, 1977: 37).

As for the source of the Arcto-Tertiary Geoflora, it is recalled that much of the temperate woody forest flora has its roots in tropical and subtropical alliances (Axelrod, 1952; see Wu, this symposium). It is probable that the early Arcto-Tertiary and late Cretaceous temperate

forest flora of conifers and deciduous hardwoods originated over middle (temperate) latitudes, especially in montane areas, and thence spread northward to high latitudes in response to cooler climate. Documentation of such a history will depend on a closer dating of presently known floras as well as finds of new ones. Certainly the temperate aspect of the early Paleocene Fort Union flora (Brown, 1962) from Montana-Wyoming-Dakota and northward, with its temperate conifers (*Glyptostrobus, Metasequoia, Taxodium*) and abundant dicots with serrate leaves as in grape, walnut, tupelo, cherry, oak, hickory, hackberry, chestnut, elm, zelkova, hazelnut, maple, and many others, is consistent with this interpretation, as is the later occurrence of more modern temperate dicots at higher latitudes. It is supported also by the more archaic character of taxa in the high arctic late Cretaceous-Paleocene floras, paralleling the persistence of a flora of "Late Jurassic-Aptian" aspect at high latitudes when early angiosperms were already in the lowlands at lower latitudes and spreading polewards (Axelrod, 1959).

The preceding distributional and phyto-sociological evidence show that in spite of slight to moderate morphological differences, the ecologic tolerances of scores of temperate taxa have not changed greatly. This statement conflicts with the notion (Mason, 1947; Wolfe, 1969: 197, 1972: 230, 1977: 47) that numerous Tertiary forest taxa have changed their physiology and have shifted to new vegetation zones. The examples purported to support this notion can be interpreted in other ways. For instance, species of *Arctostaphylos, Arbutus, Ceanothus, Cercocarpus, Colubrina, Garrya, Heteromeles, Holodiscus, Karwinskia, Lyonothamnus, Peraphyllum*, and *Umbellularia* are reported from the Miocene of northwestern Oregon. Wolfe (1969, 1972, 1977) states that they were part of a mixed mesophytic forest, not members of the subhumid Madrean sclerophyll vegetation of the southern interior to which he believes they adapted later in the Miocene. Actually, nearly all of these examples have been recorded in *older floras* of drier aspect in the southern interior. Their occurrence at the north probably was favored by the construction of Miocene volcanos along the Cascade axis, with the tuffs and breccias providing well-drained, drier sites on slopes adjacent to the rich mesic valley forests. Significantly, these taxa are essentially absent from large Miocene floras of the nearby region (Mascall, Blue Mountains, Spokane, Grand Coulee, 49 Camp, Succor Creek) that bordered local ponds and lakes formed by damming by the Columbia River plateau basalts in a region of generally low relief and high water-table.

The suggestion that the Madrean taxa from the Miocene of northwest Oregon had only a temporary, seral relation on drier volcanic slopes in that area is paralleled by distributions that resulted from the late Quaternary climatic fluctuations. Some Californian taxa that range far north inhabit the warmest, driest available sites that were invaded only since the last glacial. *Arbutus menziesii* occurs on dark (heat-retaining) metavolcanic rocks on Vancouver Island, rocks that were covered by ice only 12,000 years ago. *Quercus garryana* is confined to drier slopes in west-central Oregon and southern Washington, an area it invaded in post-glacial time (Hansen, 1942, 1947). The oak groves in the Puget Sound area are being actively invaded by *Pseudotsuga* forest and have only a seral relation (Franklin & Dryness, 1973: 89). The same relationship is implied by *Vaccinium ovatum*, a common member of the closed-cone pine forest of California that ranges northward into Washington, and was cited by Mason (1947) as an example of floristic instability. Its nearest ally, *V. confertum*, occurs in the closed-cone pine forests (*Pinus* sect. *Oocarpeae*) of Mexico where there are many related species that also make up the Californian coastal pine forests (Axelrod, 1977: 171, 1980). Ecologic studies (Franklin & Dryness, 1973: 85–86) show that *V. ovatum* borders the coastal forests to the north and has only a seral relation, occupying open, drier sites that presumably are relict from the warmer Xerothermic and more recently from logging and fire. The occurrence of these and many other typically Californian taxa far to the north has been discussed by Detling (1953, 1958, 1961) for Oregon and by Schofield (1969) who reviewed the floristic makeup of the "Mediterranean" climatic portion of southern Vancouver Island and southwestern British Columbia. As they emphasize, the "Californian" species are not an integral part of the climax conifer forests but occur in open, sunnier, drier areas for the most part, and entered this region only since the last glacial, most probably during the Xerothermic (also in Axelrod, 1966: 42–55). It thus seems unlikely that forest taxa have greatly changed their physiologic requirements, shifting to wholly new associations. Furthermore, since rapid, severe environmental shifts

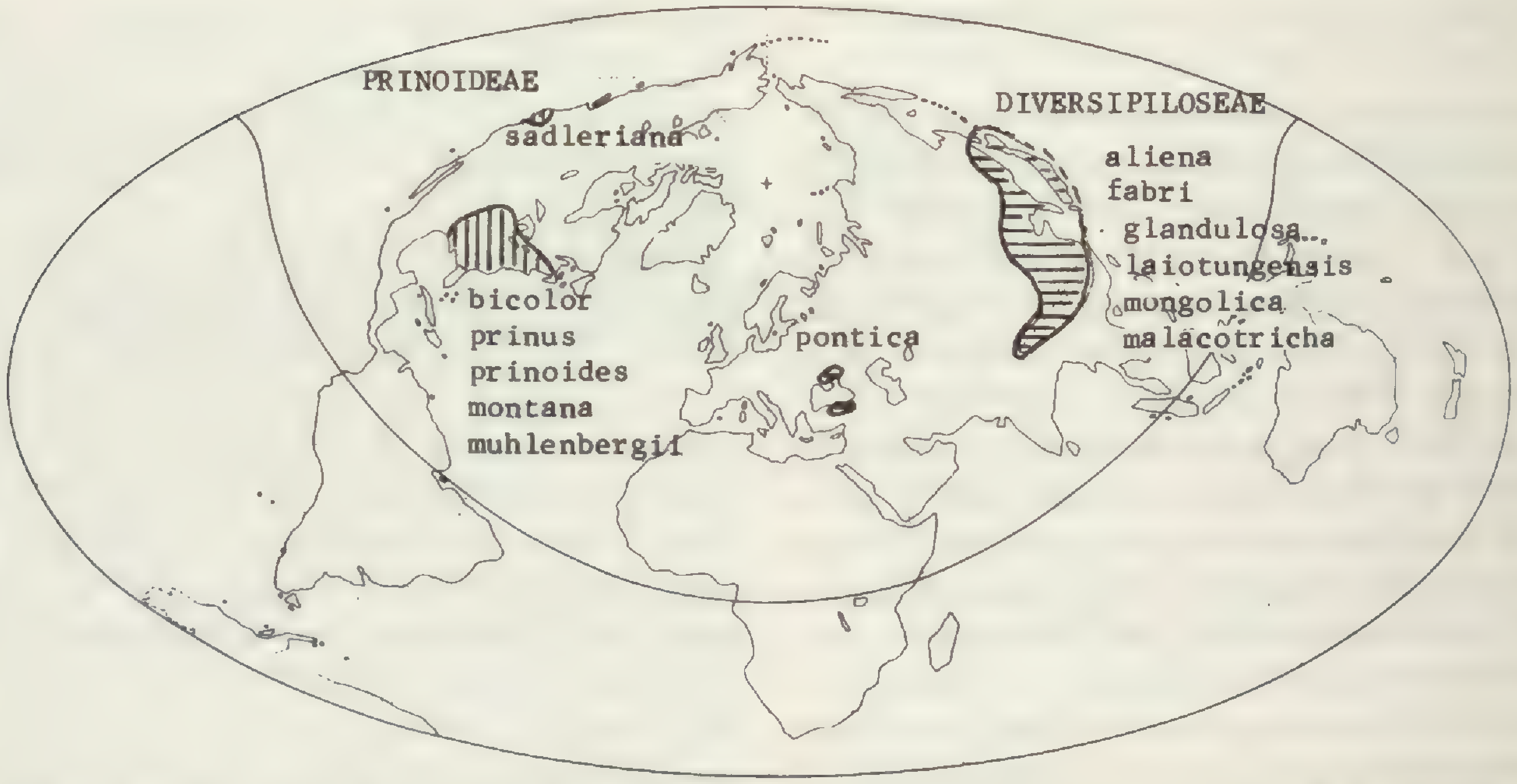

FIGURE 29. Oaks of the allied subsects. *Prinoideae* and *Diversipiloseae* are confined now to separate continents. Fossil species of these alliances were widespread across middle and high latitudes into the Miocene.

like those of the Quaternary are not documented for the Tertiary, there probably was little interchange between North America and Eurasia of taxa that represent sections of genera that originated in restricted parts of one continent or the other.

This is not to deny that taxa may have shifted to new associations, but these were between the same general forest types, as in the shift of a taxon from the American to the Asian sector of the mixed deciduous or conifer-hardwood forest. Examples of such shifts are not readily demonstrable today because the record is still too incompletely known to determine whether a fossil species in western North America moved to eastern Asia or *vice versa*. An ancestral species may have moved southward and changed more in one area ("derived") than the other, thus giving rise to the impression that the "primitive" form migrated to give rise to the "derived" taxon. Clearly, the notion that taxa have commonly moved into associations widely different from those in the ancestral community is not demonstrated. Some taxa have been restricted upward, out of

FIGURE 30. Distribution of species of *Erythrobalanus* subsect. *Rubrae*. Taxa similar to *coccinea* and *palustris* occur in the Miocene of Oregon. Oaks of this group have also been divided into subsects. *Laeves*, *Ilicifoliae* *Palustres*, *Coccineae*, *Pagodaefoliae*, and *Californicae*.

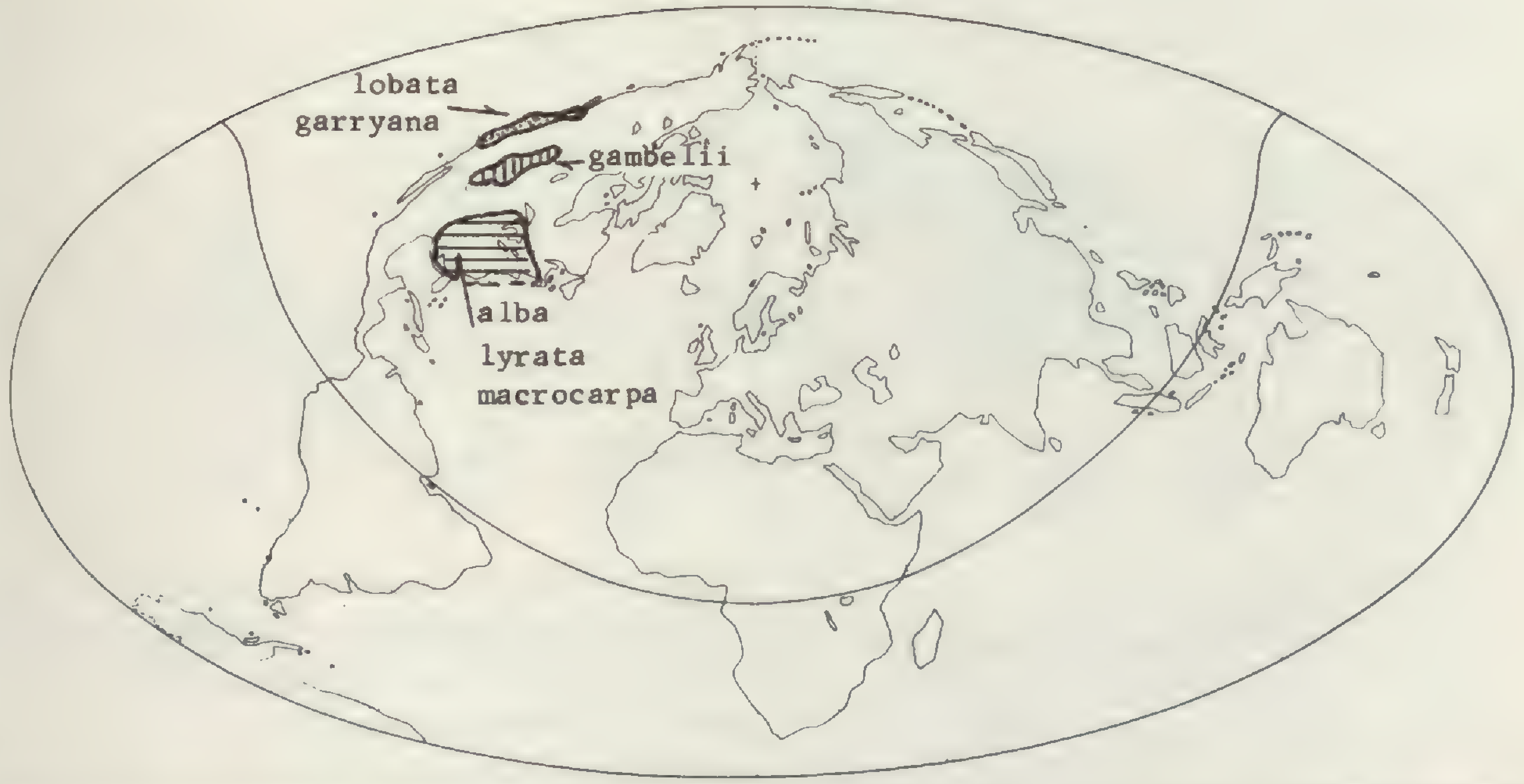

FIGURE 31. Lobed white oaks have been divided into subsects. *Lobateae, Gambelieae, Albeae.* Those of the former two occur as fossils in the far West during the Miocene. Members of *Albeae* have not yet been certainly recorded there.

associations now too xeric for them, and others have moved to lower elevations where climates are warmer, but in such cases they are still components of associations in which they were present formerly. That is, upland taxa forest earlier reached to lower levels and sclerophyll taxa to higher ones under a climate of ample summer rain and milder winters (Axelrod, 1976, fig. 4).

Past and Present Distribution of Oaks

The preceding data provide a basis for interpreting the Tertiary history of oaks in the Arcto-Tertiary province. Figures 29 to 37 illustrate the present concentrations of some representative species of several *Quercus* sections (from Trelease, 1924; Camus, 1936–54) and Tables 1 to 3 indicate the present distribution of oaks in the temperate regions chiefly. It is apparent that whereas species of many sections or subsections of dicots have ranged widely across Holarctica (see above, Figs. 1–16), only members of the allied subsects. *Prinoideae* and *Diversipiloseae* occurred throughout temperate Holarctica during the Tertiary and earlier, having been recorded in Spitzbergen, Iceland, Alaska, Siberia, and also

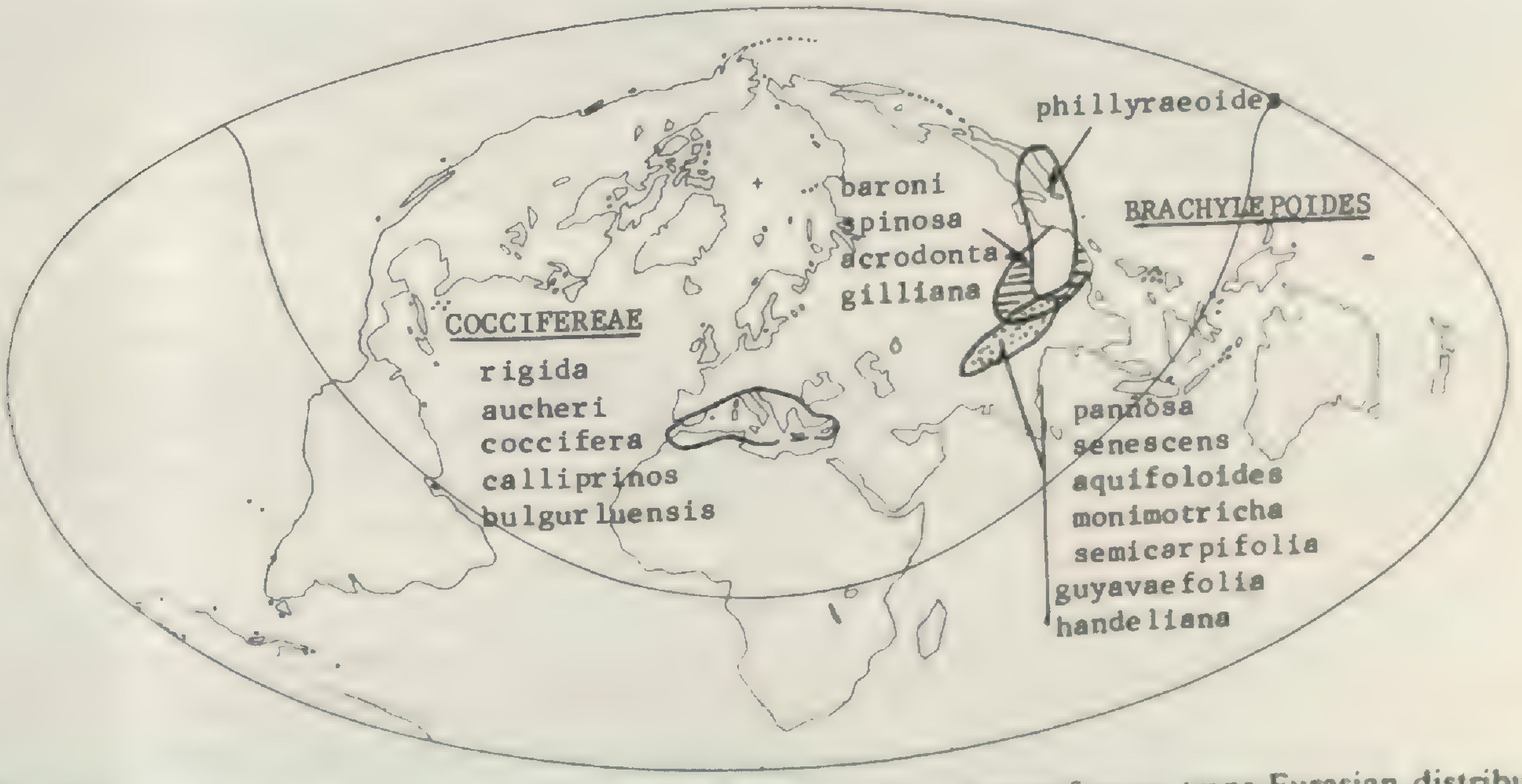

FIGURE 32. Oaks of sect. *Cerris* represent two subsections that imply former trans-Eurasian distribution. Fossils of each subsection have been recorded in their respective areas during the Neogene.

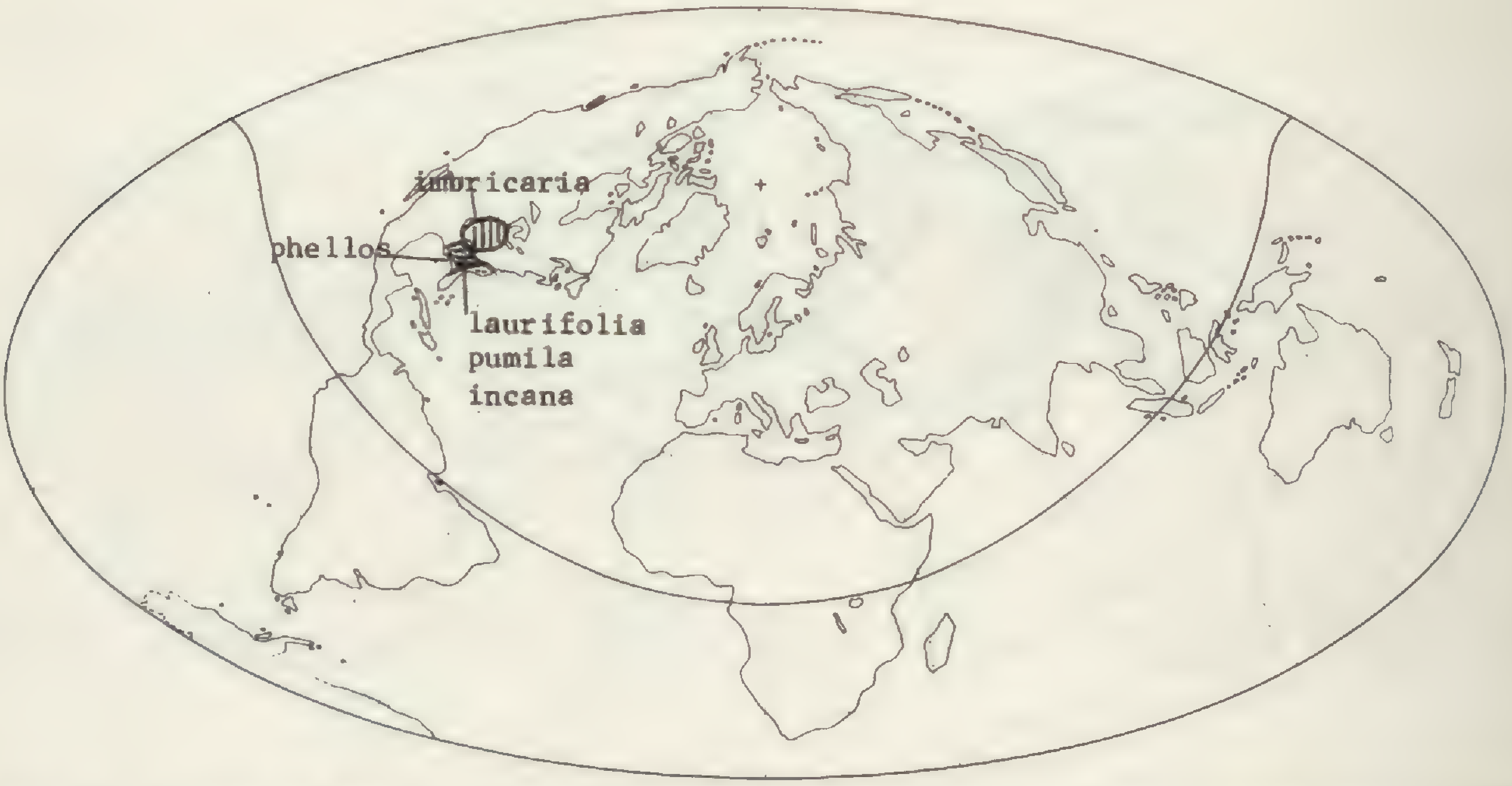

FIGURE 33. Taxa of subsect. *Phellos,* confined now to the southeastern United States, were represented by species allied to *phellos* and *imbricaria* in the Miocene of Oregon.

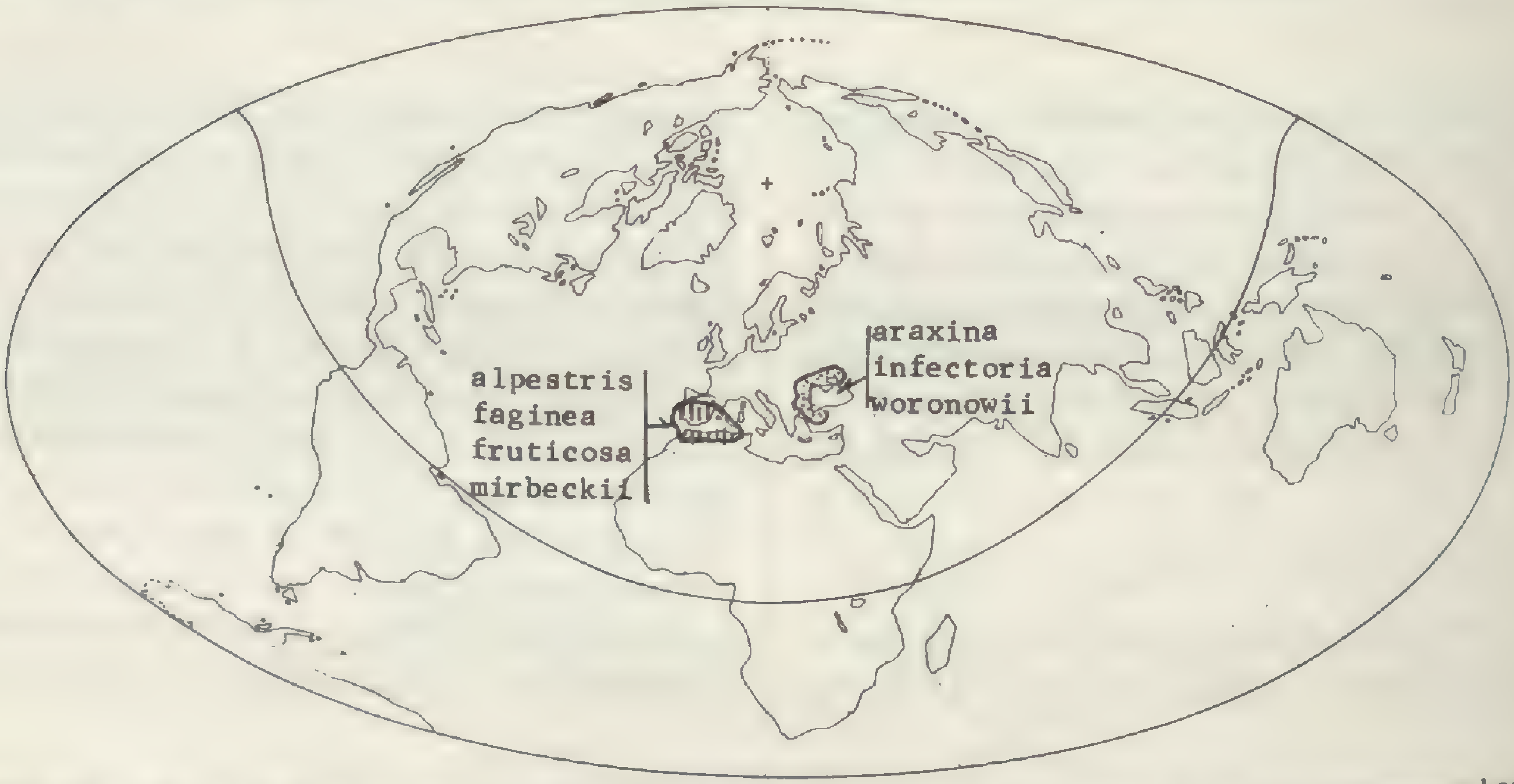

FIGURE 34. Taxa of *Quercus* subsect. *Galliferae* are recorded in the Neogene of the Mediterranean basin.

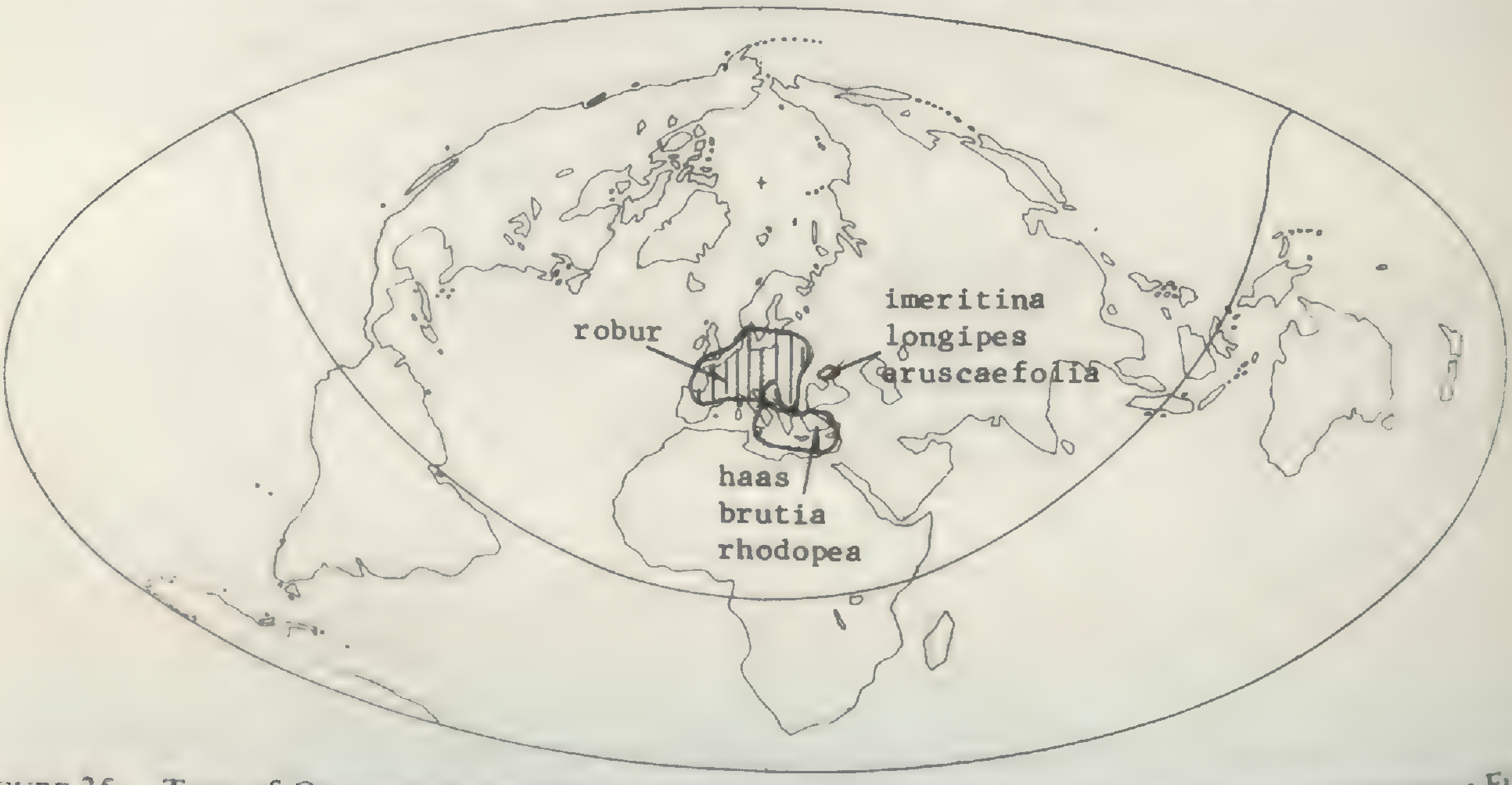

FIGURE 35. Taxa of *Quercus* subsect. *Pedunculateae* are recorded as fossil in the Neogene of western Europe. Three endemics are in the Caucasus Mts.

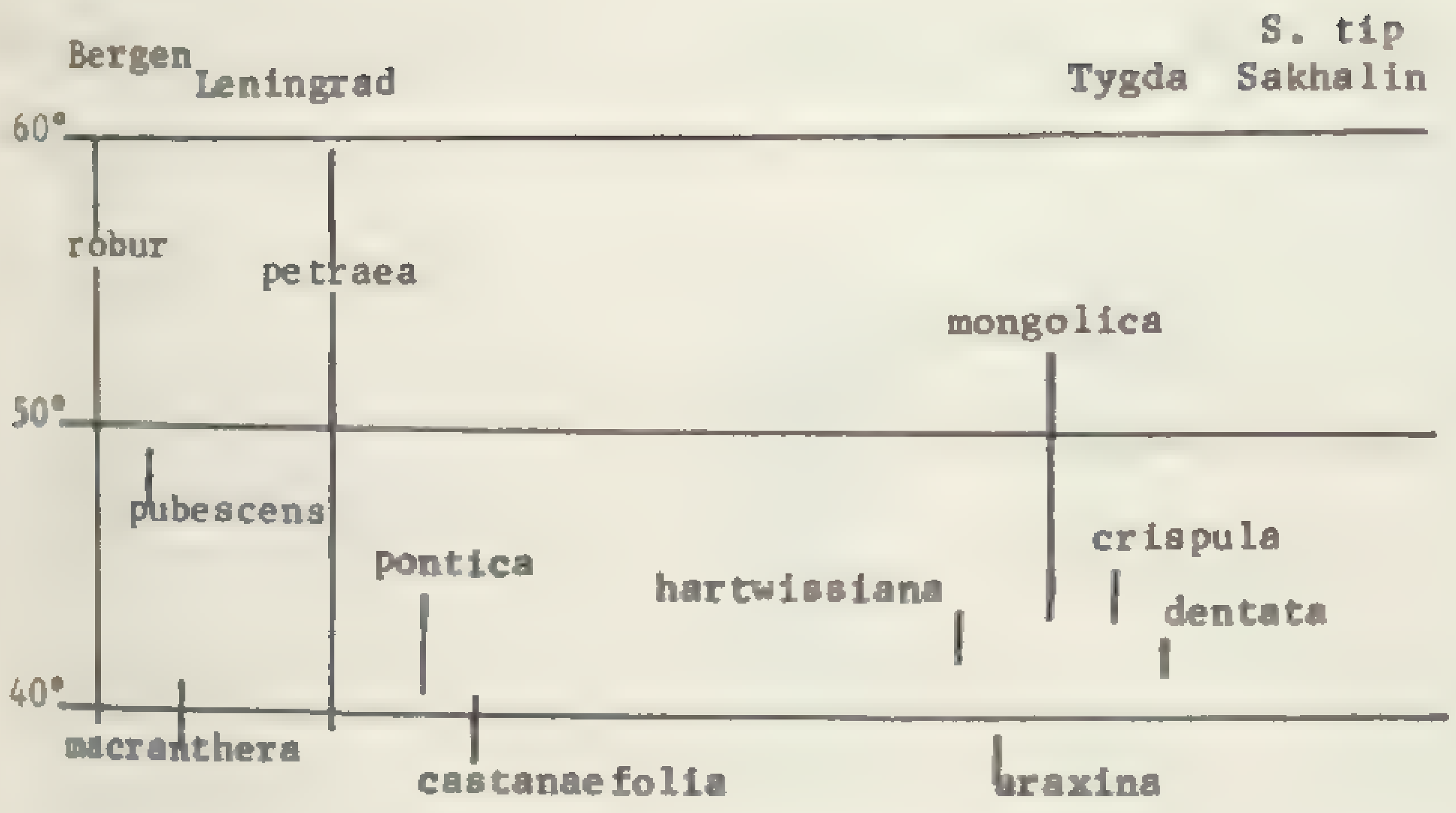

FIGURE 36. Northern limit of Eurasian oaks today.

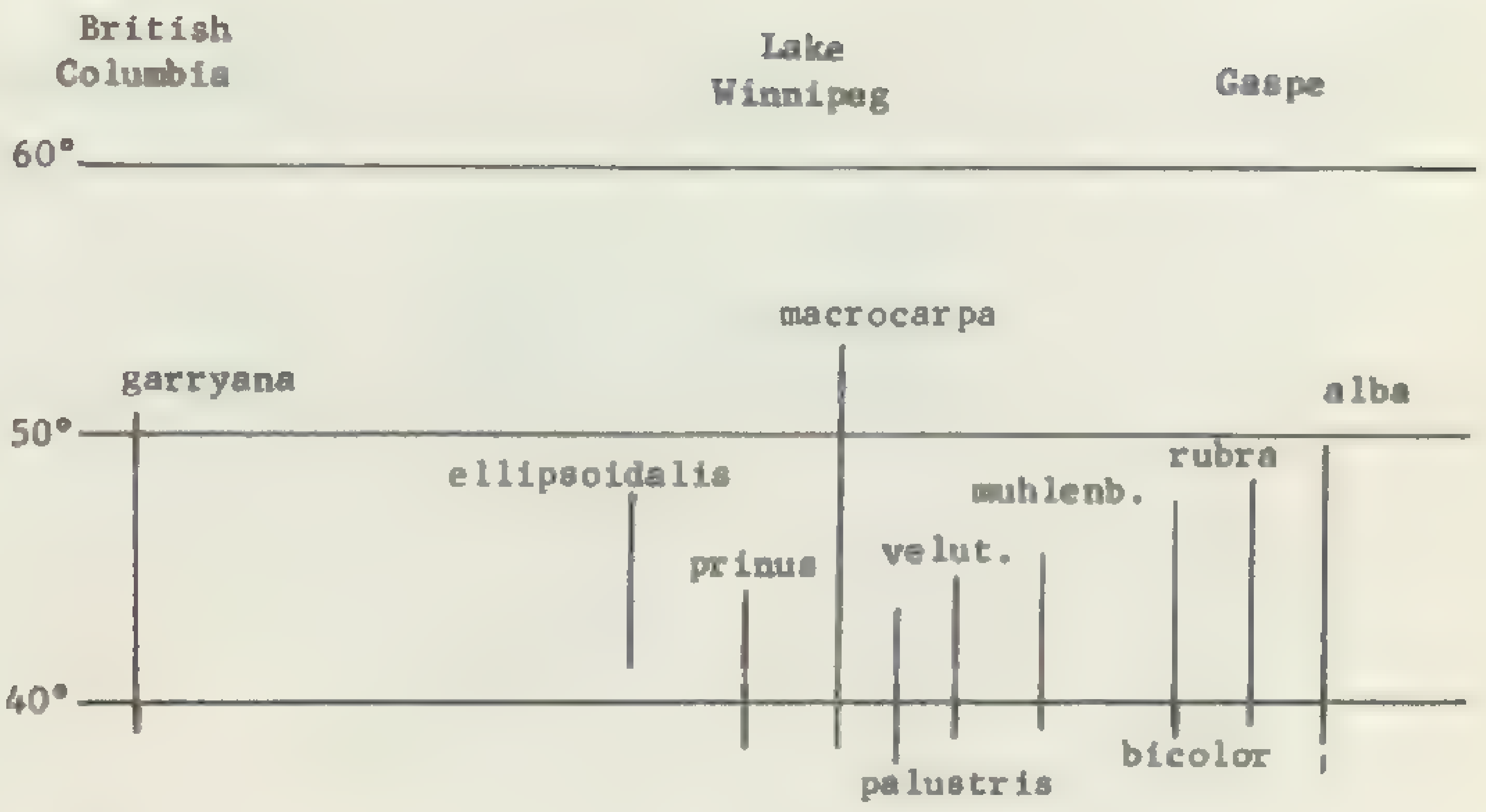

FIGURE 37. Northern limit of American oaks today.

at middle latitudes in Eurasia and western North America. The presence of these allied subsections (or series) on separate land masses today and the records of similar fossil species in the far north in the early Tertiary implies a southward shift in response to cooling climate and the resultant divergence of two closely allied groups. The alliance was already at middle latitudes by the Paleocene (Brown, 1962, pl. 19) and a fossil species of *Prinoideae* is in the Bull Run flora (40 m.y.a.) of northern Nevada, where it contributed to conifer-deciduous hardwood forest at an elevation close to pure subalpine conifer forest.

Species of most sections and subsections of *Quercus* are restricted to one continent or to specific parts of it, paralleling those discussed for other dicots (see above). Their close fossil allies occurred more widely in the Neogene but most did not range far from their present areas, as judged from the record in Europe, Asia Minor, Japan, China, and western United States (Figs. 1–5). Examples of wider distribution in the far West are provided by the records of red oaks (aff. *coccinea, falcata, velutina*) and chestnut oaks (aff. *bicolor, prinus, muhlenbergii*) in Washington, Oregon, and Idaho. Species of sect. *Cerris* occur widely across southern Eurasia and the species east and west represent different subsections (Fig. 32), implying an ancestral alliance adapted to different climates differentiated in them as conditions changed. Most subsections in the genus (as now recognized) display only local occurrences, as shown by subsects. *Robur* (= *Pedunculatae*) (Fig. 35), *Phellos* (Fig. 33) and many others. Their taxa have not ranged far from their present areas, which have been restricted by spreading dry climate that compelled forest and woodland species to retreat into locally favorable, often montane, habitats (Axelrod, 1979). As noted by Trelease (1924), the Californian and Rocky Mountain white oaks are unlike those of the Atlantic region, and the black oaks of the California province are distantly related to those of eastern North America and are remote from those of Mexico-Central America. The relations imply that these oaks originated in relatively local provinces.

Fossil evidence for restriction of species of most subsections (series) to comparatively local regions and with little or no continental interchange during the middle and later Tertiary is consistent with systematic evidence (Tables 1–3). Furthermore, the restriction of most sections to their present continental areas, or to parts of them, is clearly shown by illustrations of the numerous fossil oaks from across the USSR which are of Eurasian affinity (Takhtajan, 1982). As Trelease noted (1924), "the existing oaks of temperate regions have developed since the breaking of the circumpolar land connection of Tertiary time: that the genus may have penetrated Europe by way of the Orient in *Cerris* and *Ilex* types; and that it may have reached America originally over one or more now vanished land connections . . . ."

Cretaceous links are implied by the occurrence of *Lithocarpus* and *Castanopsis* (= *Chrysolepis*) in California, which are allied to Asian taxa in warm temperate climates. Furthermore, *Lithocarpus* (as *Q. nevadensis* Lesq. and a distinctive acorn cup) was already present in California in the late Early Eocene Chalk Bluffs flora. Together with the disjunct occurrence of *Trigonobalanus* (Yunnan-Thailand-Borneo to Colombia), connections are implied across the Atlantic (1) when it was narrower than at present and prior to the counter-clockwise rotation of North America, and (2) when more numerous, now-sunken islands linked these regions (Axelrod, 1972, fig. 25, 1979; Raven & Axelrod, 1974).

NORTHERN LIMIT OF *QUERCUS*

Available evidence indicates that most oak species have not followed many widespread taxa

Table 1. Distribution of sections and subsections of *Quercus* in Holarctica (from Camus, 1936–54).

	Europe	Mediter. Basin	Asia Minor & Persia	Himalayas (to Afghan-istan)	S. China (Yunnan)	C. China	NE Asia–Japan	
Subgenus Cyclobalanopsis				x	x	x	x	(To Malaysia-Borneo)
Subgenus Euquercus								
Sect. Cerris								
Subsects.								
Brachylepides (15 sp.)				x	x	x	x	(To upper Burma)
Echinolepides (3 sp.)				x	x	x		
Cypriotes (1 sp.)		(Cyprus)						
Cocciferae (4 sp.)		x	x					
Suber (1)		x						
Macrolepides (9)		x	x					
Campylolepides (2)					x	x	x	
Eucerris (1)	x	x						
Sect. Mesobalanus								
Subsects.								
Malacolepides (1)							x	
Macrantherae (3) (excl. Ponticae)	x	x	x				x	
Sect. Lepidobalanus								
Ser. 1. Gerontogeae								
Subsects.								
Floribundae (6)				x	x	x		(To Annam)
Pachyphyllae (5)				x	x			(To Assam, Siam)
Englerianae (1)					x			
Ilex (1)	x	x	x					
Diversipilosae (9)			x		x	x	x	
Galliferae (5)		x	x					
Hartwissianae (1)			x					
Sessiliflorae (6)	x	x	x					
Lanuginosae (2)	x	x	x					
Pedunculatae (7)	x	x	x					

TABLE 2. Distribution of sections and subsections of *Quercus* in North America (from Camus, 1936–54).

	Calif.	Baja Calif.	Ariz.-Texas-Colo.	Central US	Southern US	E US–(Canada)	
Sect. Lepidobalanus							
Ser. 2. Americanae[a]							
Subsects.							
Virentes (6)		x	(W. Tx)		x		(To E. Mexico)
Dumosae (2)	x	x	x				
Griseae (1)			x				
Oblongifoliae (2)	x	x	x				
Undulatae (3)			x				
Arizonicae (3)			x				
Douglasiae (1)	x						
Confusae (4)			x				
Lobatae (2)	x		x				
Gambelieae (3)			x				
Prinoidae (7)	x			x	x	x	
Stellatae (3)				x	x		
Lyratae (1)				x	x	x	
Albae (1)				x	x	x	
Macrocarpae (1)			(relict)	x	x	x	

[a] Excluding subsects. in Mexico–Central America; also sect. Macrobalanus, first ten subsects. are Madrean in origin.

in terms of a broad Holarctic occurrence during the Tertiary; most species and subsections (or series) have had relatively restricted distributions. Fossil oak remains are not common in Tertiary floras from higher latitudes, as Greenland, Spitzbergen, Ellesmereland, Alaska, or Sakhalin. Those that have been illustrated readily fall into subsects. *Prinoideae* and *Diversipiloseae*, the leaves resembling those of *Q. prinus, aliena, muhlenbergii, mongolica,* and their allies. This raises the problem as to why other fossil oaks are rare (or absent) in floras from latitudes generally above latitude 50°N. Oaks now reach their northern limit near latitude 50°N (Figs. 36, 37) and only *Q. robur* and *petraea* extend to latitude 60°N in the Baltic region, an area they no doubt invaded during the Altithermal. Temperature is not the chief factor that accounts for their rarity at high latitudes in the Tertiary. Those areas supported rich deciduous forests (Figs. 1–16) into the Middle Neogene (15–16 Ma), yet the only oaks encountered there are those of *Prinoideae-Diversipiloseae*. Most oaks occupy latitudes well below 40°N and the highest concentrations are in latitudes 15–30°N, in Mexico-Central America (with some 150 species), and southeastern China. Judging from Figure 38, light may be the principal factor that limits, and has limited, the northern distribution of most oaks. In this regard, it seems significant that of the 18 species that now reach latitude 45–50° (Figs. 36, 37), five are members of the *Prinoideae-Diversipiloseae*, which had a wider distribution in the Paleocene and later, reaching above latitude 60°N into the middle Miocene.

EVOLUTION

Oaks comprise one of the more active groups of woody plants in terms of evolution during the Tertiary. There are now about 280 to 300 species and scores of hybrids are recognized. The great plasticity of the group is apparent in the convergence in similar leaf form and acorn type among species belonging to different sections of the genus. Oaks proliferated in generally restricted regions, chiefly in response to increasing topographic, climatic and edaphic diversity during the middle and later Tertiary. In addition, there were certain times when climatic extremes increased sharply, as at 35, 13, and 5 Ma (refs. in Axelrod, 1981; Kennett, 1981), as well as during Quaternary fluctuations. These major climatic shifts may have corresponded with times of especially rapid speciation in oaks (and other taxa) as older alliances disappeared and more open communities became available.

An example of such a radiation is suggested by the history of *Quercus wislizenii* and its close

Table 3. Distribution of sections and subsections of *Quercus* in North America (from Camus, 1936–54).

	California	Arizona	N. Baja Calif.	N. Mexico	Southern US	Central US	Eastern US	NE US & Canada
Sect. Protobalanus (6)	x	x	x					
Sect. Erythrobalanus[a]								
Subsects.								
Durifoliae (1)		x		x				
Agrifoliae (2)								
Vimineae (1)				x				
Hypoleucae (1)		x		x				
Saltillenses (3)				x				
Myrtifoliae (1)					x			
Phellos (5)					x	x	x	
Marylandicae (3)					x	x	x	x
Laeves (1)					x	x	x	
Pagodaefoliae (2)					x			
Ilicifoliae (1)							x	x
Palustres (2)						x	x	x
Velutinae (1)					x	x	x	x
Coccineae (4)				x	x	x	x	x
Californicae (1)	x (to S. Oregon & Baja Calif.)							

[a] Excluded are all subsects. in subtropical Mexico–Central America.

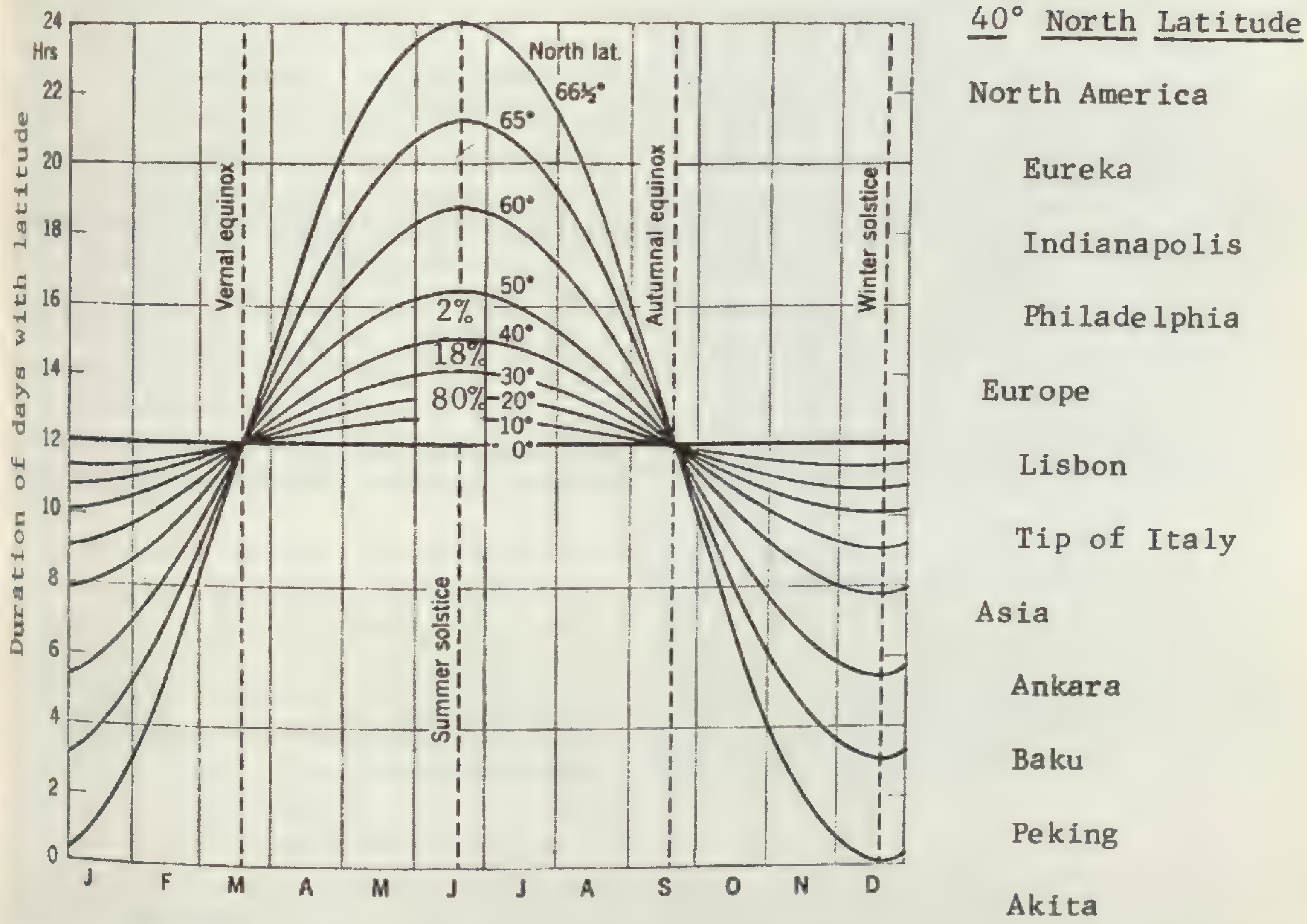

FIGURE 38. Most oaks are adapted to short days at lower latitudes. Percentage figures indicate the approximate representation of oaks in the indicated latitudinal belts. (Figure from Strahler & Strahler, 1977, with permission of J. Wiley & Sons.)

allies, *Q. shrevei, parvula,* and *frutescens* (Fig. 39). In California and Nevada there are large suites of fossil leaves of two members of the complex, *Q. wislizenoides* and *Q. shrevoides* ined., that are similar to those produced by the living *Q. wislizenii* and *Q. shrevei.* The fossils commonly form the dominants to subdominants of the floras in which they occur. Figure 39 shows that the alliance appears first as *shrevoides* in west-central Nevada and shifts westward to Sierra Nevada (Remington Hill flora) and is now (as *Q. shrevei*) in the outer south Coast Ranges of California. As climate became drier, *wislizenoides* replaced *shrevoides* in western Nevada (Verdi, Truckee floras) and then in the lower Sierra Nevada and the inner Coast Ranges. The shifts in adaptive type seem related to major environmental changes in the upper Miocene (13–12 Ma) and in the latest Miocene (5–6 Ma). There has clearly been a coastward restriction from the present Nevada desert of the presumed ancestral *Q. shrevoides-shrevei* line which has contributed to mesic broadleaved sclerophyll forest for fully 18.5 million years. *Quercus wislizenoides-wislizenii* have typified semiarid oak-grassland woodland vegetation since the later Miocene, shifting from Nevada into California as conditions became drier and cooler to the east as the Sierran block was elevated. Fossil records of the shrubs are not now known, but their ecologic relations suggest that *parvula* is older than *frutescens.*

As for their origin, oaks of the *wislizenii* alliance are related to the series *Peninsulares* Trelease (*Q. peninsularis, Q. devia*) of Baja California. *Peninsulares* are allied to *Durifoliae* (*Q. emoryi, durifolia*) of the southwestern United States and northwestern Mexico, and to the *Vimineae* (*Q. bolanyosensis, duranzillo, balsequillana, viminea*) of the northern Sierra Madre Occidental. The *Peninsulares, Durifoliae,* and *Vimineae* represent taxa adapted to subhumid to semiarid areas with summer rain; whereas *Q. shrevoides* and *wislizenoides,* which lived earlier under biseasonal rainfall, have adapted to the dominant winter-rain climate of California. *Peninsulares* were restricted to their present area

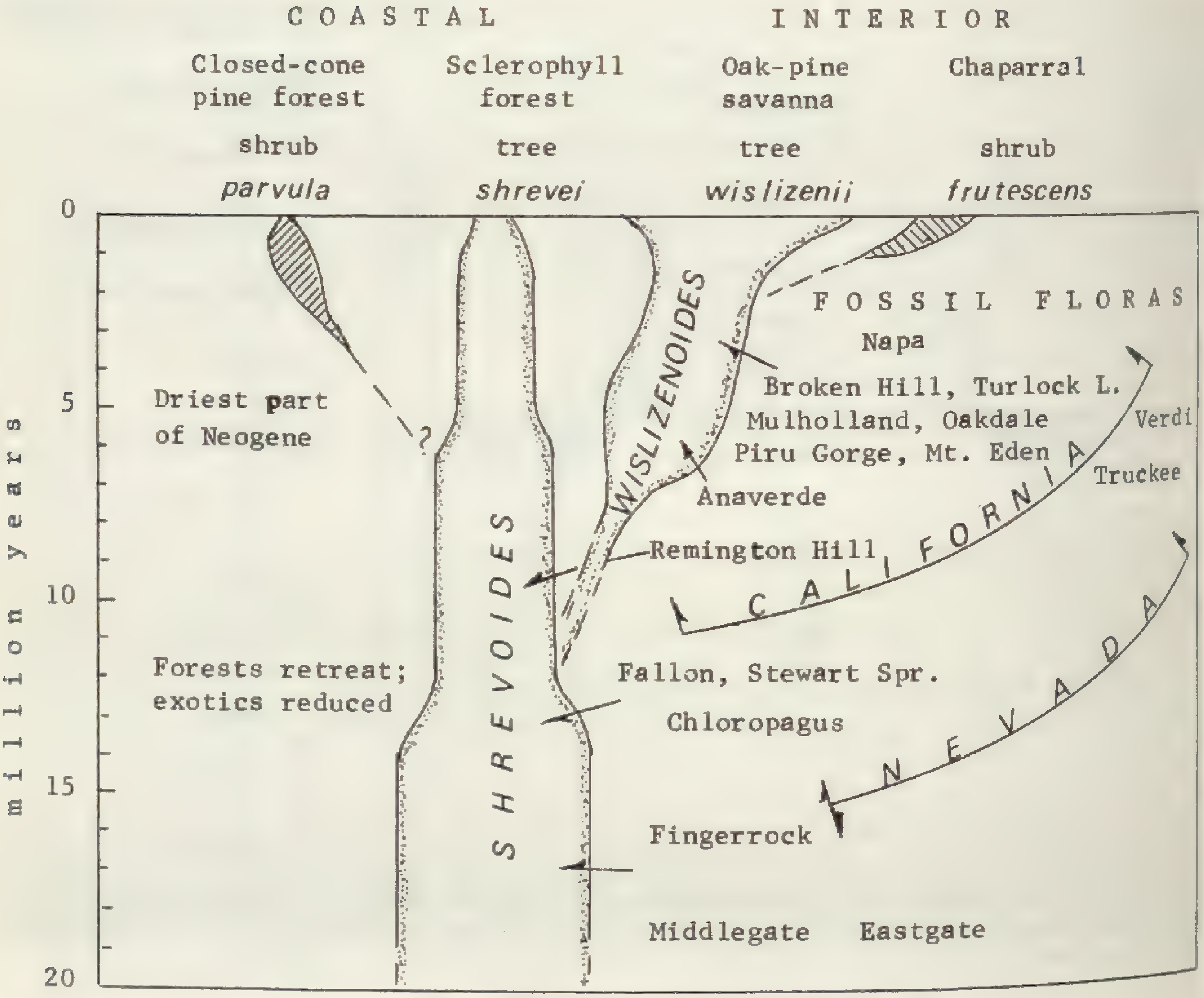

FIGURE 39. Inferred relations of oaks of the *Quercus wislizenii* complex (see text).

as the lowlands became drier; they live in a young mountainous region, one elevated only in the last two to three million years (Gastil et al., 1975). The *Durifoliae* ranged more widely in the past, as shown by records of fossil oaks allied to *Q. emoryi* in the Tehachapi (17 Ma) and Mint Canyon (12 Ma) floras, southern California. The preceding data imply that these series probably are ancient and survived in favorable environments as drier climates spread more widely in the late Cenozoic. To judge from the modern aspect of oaks of subhumid requirements in the Florissant flora (34 Ma), the *wislizenii* complex and its allied series may have diverged from an ancestral alliance in Oligocene time.

The present disjunct subsections of sect. *Cerris* and *Suber* across Eurasia and of the *Albeae* (incl. *Lobateae*) and *Rubreae* (incl. *Coccineae*) across the United States also reflect restriction following the spread of drier climate and of a shift in seasonal rainfall distribution in the far West. Marked aridity had developed over southwestern Asia and North America by the middle Eocene. This may have been the time of origin of some of the major subsections (or series) of the genus. Dry climates commenced to spread rapidly in the middle Miocene as the Tethys Sea was destroyed and as ice spread on Antarctica (13 Ma). Forest taxa now retreated into rapidly rising mountains and differentiated east and west into new subsections (series) and many species. The presence of new upland terrains and their accompanying local climatic differences may well have provided a basis for the origin of numerous distinctive taxa as founder populations exploited these novel environments. With rapid shifts in climate and instability in populations, the effect would have been the rapid origin of distinct taxa, thus simulating the phenomena of punctuated equilibria.

In the central Cordilleran region of the United

States, sequences of floras from the middle Eocene to the early Miocene (Green River, Florissant, Beaverhead, Ruby, Creede) show that numerous taxa (i.e., *Cercocarpus, Colubrina, Mahonia, Peraphyllum, Philadelphus, Rhus, Sapindus,* many small legumes) that imply drier climates were spreading over the area. A small-leaved, lobed Eocene white oak (*Q. lyratiformis* Cockerell) in the Florissant flora (35 Ma) is the only record of the group in older floras (Fig. 40). It may be suggested that it spread east and west into moister terrains, developing into larger-leaved species in eastern (*alba, macrocarpa, lyrata*) and western (*lobata, gambelii, garryana*) areas.

The problem of the origin and relationships of the lobed red (black) oaks, subsects. *Coccineae-Rubreae* (incl. *Q. kelloggii*), is not readily solved today. The oldest black oak is the early Eocene Chalk Bluffs *Q. eoxalapensis* MacGinitie (1941), but it appears quite unlike an ancestral type for *Coccineae-Rubreae.* A possible ancestral form may be *Q. peritula* Cockerell from the late Eocene Florissant flora (MacGinitie, 1953) (Fig. 40). If it spread east and west into more humid climates and developed larger leaves, it may have given rise to *Coccineae-Rubreae.* On this basis, the species east and west of the Cordillera would have differed in some respects. The western Miocene fossil species, some undescribed, show relationship to *Q. falcata, coccinea* and *velutina* of the eastern United States and to *Q. kelloggii* of the west. The moderate differences east and west may express no more than foliar plasticity in the group. It is also evident that in some floras (Mascall, Stinking Water) there appears to have been hybridization among the lobed oaks.

RADIATION

Some natural subsections have radiated into very diverse environments. For instance, species of sect. *Chrysolepideae* occur in several vegetation zones. *Quercus tomentella* is a woodland tree endemic to islands off southern California and to Guadalupe Island; it occurs with closed-cone pine forest on Santa Cruz and Guadalupe Islands. *Quercus cedrosensis* is a shrub in coastal sage, chaparral, and closed-cone pine vegetation zones on the coastward slopes of northern Baja California. *Quercus dunnii* is a co-dominant of the chaparral of southern California and southern Arizona. *Quercus chrysolepis* is a large, wide-spread evergreen tree that dominates the mixed evergreen forest (sclerophyll forest) of California and enters the lower part of the adjacent mixed conifer forest in rocky canyon walls and exposed areas. *Quercus vaccinifolia,* clearly derived from *Q. chrysolepis,* ranges from the upper mixed conifer forest into fir-subalpine forest and locally reaches close to tree-line. These taxa occur in areas with precipitation as low as 300 mm (12 in.) and as high as 2,500 mm (100 in.) and the montane sites have heavy snow. The growing season may last fully seven months (Ensenada) or be as brief as two to two and a half months (above Twin Lakes, California).

In sect. *Cerris* subsect. *Brachylepides,* which is largely in the area from central China to Yunnan, *Q. semicarpifolia, aquifoloides, pannosa,* and *gilliana* range up to 3,000 to 4,000 m in Yunnan. Since the age of the mountains is established, the rate of adaptation of these taxa to high montane conditions, and their derivation from ancestral species, can be estimated. Clearly, field studies of radiation of natural cohorts in *Quercus* can be quite rewarding.

DOMINANCE

Evidence in northeastern Asia suggests that although *Q. mongolica* was present there (as *Q. protodentata*) as a regular member of the Miocene rich deciduous forest, pollen studies indicate that the present oak forests dominated by *Q. mongolica* are late Quaternary (in Ablaev & Gorovoi, 1974). A similar relationship is indicated for the dominant lowland oak communities in California and Arizona as judged from late Pleistocene fossil floras and from evidence provided by wood-rat middens. Fossil species allied to *Q. agrifolia, douglasii, engelmannii,* and *wislizenii* are recorded in Miocene and Pliocene floras as members of rich sclerophyllous woodland. The living species that form pure stands at low elevations adjacent to grassland have adapted to these drier areas more recently and represent new monoclimax communities. A similar relationship is indicated for *Q. emoryi* and *Q. oblongifolia,* which dominate as pure communities at the edge of grassland and above the desert which supported rich woodlands into the latest Pleistocene.

SUMMARY

The preceding review of the present distribution of oaks and areas of their fossil occurrence leads to the following tentative conclusions.

1. The Fagaceae, which probably originated in

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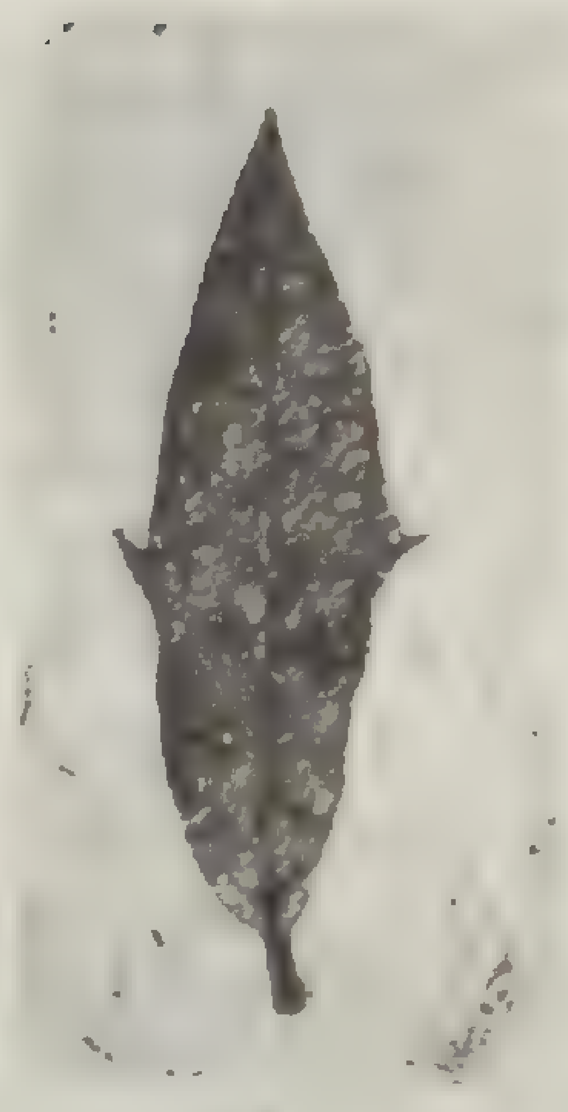

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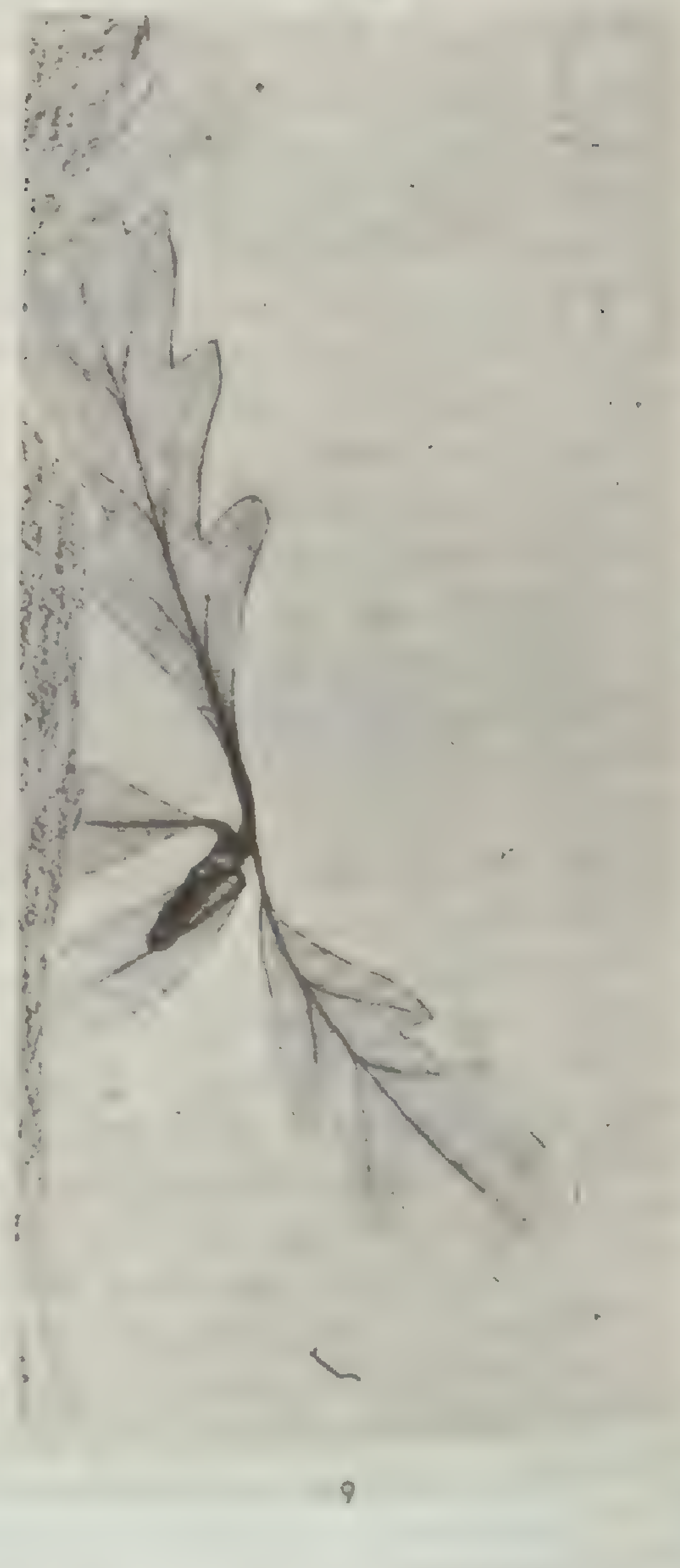

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the montane tropics, had migrated across the tropics via the Atlantic and had diverged into the principal living genera by the later Cretaceous.

2. Following the Eocene, oaks underwent rapid evolution chiefly in regions of mild to warm temperate climate as cooler and drier conditions spread and especially in areas where terrain diversity was increasing rapidly, as in Mexico-Central America, the southwestern United States, the Mediterranean basin and southeastern Asia.

3. Oaks were rare at higher latitudes during the Tertiary even though temperature was mild and well suited for numerous deciduous hardwoods and conifers. Northward distribution of most oaks evidently was controlled primarily by light (long day) north of latitude 50°.

4. Many sections and subsections (or series) are confined to local sectors of the continents and for the most part their antecedents have inhabited the same general areas, although they ranged more widely prior to the spread of grassland and desert climates. This is paralleled by sections of other genera (i.e., *Acer, Alnus, Betula, Pinus*) that occur locally on the continents, although other sections of these and many other genera have been and are still widespread on the continents. Also linking the present disjunct forests are numerous allied forest herbs, many of which have changed only slightly since the Miocene. Together with the trees and shrubs they form the broken floristic threads that make up the surviving matrix of the temperate Arcto-Tertiary Geoflora, whose demise has been certainly misrepresented.

5. Few oaks have linked North America-Eurasia, consistent with their evolution in generally restricted parts of the continents. Only the allied subsects. *Diversipiloseae* and *Prinoideae* have occupied higher latitudes and their derived species still occur on all the northern continents. Taxa of only a few sections have ranged across North America or Eurasia, notably *Albeae, Coccineae,* and *Virentes* in the former, *Cerris, Suber,* and *Cyclobalanopsis* (probably) in Eurasia.

6. The rise of oaks to dominate temperate forests and woodlands appears to be a phenomenon of the later Cenozoic, one afforded by selection for greater drought and higher temperature at lower levels (California-Arizona, Spain-Turkey) and by cold in the interior (Manchuria-Primorye, central U.S.).

7. Species of subsections (series) of *Quercus* radiated from subtropical and warm temperate into subalpine environments as mountains were elevated in the late Tertiary; ecologic studies of these cohorts should prove illuminating.

8. Further progress in understanding oak evolution will depend not only on obtaining additional fossil plants and re-evaluating those in older collections, but also on taxonomists providing a more realistic grouping of taxa into natural alliances.

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Figure 40. Small-leaved sclerophyllous oaks had appeared over the central Cordilleran region by the close of the Eocene. These are from the Florissant flora (MacGinitie, 1953).—1, 4. *Q. scudderi* Knowlton;—2, 3. *Q. edavana* MacG.;—5, 6. *Q. mohavensis* Axelrod;—7, 8. *Q. peritula* Cockerell;—9. *Q. lyratiformis* Cockerell (natural size).

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GENETIC DIVERGENCE WITHIN THE GENUS *LIRIODENDRON* (MAGNOLIACEAE)[1,2]

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ABSTRACT

The genus *Liriodendron* L. consists of a southeast Asian–eastern North American disjunct species pair, but the genus had a much wider distribution in the Northern Hemisphere during the late Cretaceous and the Tertiary. Although generally similar in morphology, the two extant species are measurably different. In 1973 and 1977 they were hybridized, and interspecific heterosis was observed in the progeny. After seven years, the interspecific hybrids synthesized in 1973 had a significantly greater biomass than intraspecific hybrids of *L. tulipifera*. The growth rate of interspecific and intraspecific F_2 seedlings was approximately equal. A preliminary survey of flavonoid extracts in *L. tulipifera* populations showed a high level of quantitative variation that was not obviously correlated with either geographic or environmental parameters. While there was little flavonoid variation in one small *L. chinense* population, a tree from a second locality in China was markedly divergent in its chromatographic pattern. An isozyme survey of individual trees from a few populations showed *L. tulipifera* to be moderately heterozygous. Six trees of *L. chinense* from one locality were identically homozygous, while a seventh tree from a different locality was equally homozygous but for different alleles at a number of loci. The available evidence indicates that the two *Liriodendron* species have not diverged very far from a presumed common ancestor. However, *L. tulipifera* is an abundant, almost weedy, species in some parts of its range, whereas *L. chinense* has suffered from population restriction and loss of heterozygosity to the degree that it shows inbreeding depression.

The genus *Liriodendron* includes two extant species, *L. chinense* (Hemsl.) Sarg. and *L. tulipifera* L., and a number of extinct species that are based on fossils of leaves or seeds from various Cretaceous and Tertiary strata. The Chinese tulip tree occurs in widely scattered populations from the northern part of Indochina to the eastern Chinese provinces of Anhwei and Hupeh (Fig. 1). From conversations with botanists from the People's Republic of China, it appears that *L. chinense* exists as a small number of populations each containing only a few individuals. Unlike the Chinese species, *L. tulipifera* is abundant and often weedy over much of its range, which includes nearly all of the United States east of the Mississippi River (Fig. 1).

Fossils in deposits of Tertiary age from Asia, Europe, and North America indicate that *Liriodendron* was once much more widely distributed in the Northern Hemisphere. It survived in Europe at least until the Pliocene and early Pleistocene (Szafer, 1954), and is represented in western North American Paleogene (Wolfe, 1972) and Neogene sediments (Smiley & Rember, 1981). Considering this paleobotanical evidence, it is probable that *Liriodendron* was widespread in the Northern Hemisphere in what has been termed the Arcto-Tertiary Forest (Chaney, 1959), and that its present distribution reflects range restrictions due to local extinction at various times in the late Cenozoic. There is no evidence that populations of contemporary *L. tulipifera* and *L. chinense* were ever sympatric, although these taxa may survive as relicts of antecedents whose distribution was originally sympatric.

Despite the long isolation, the two extant species are highly interfertile (He & Santamour, pers. comm.; Santamour, 1972; Miller & Parks, 1980). In 1973 two of us (Miller & Parks) set up a long-range hybridization study to explore the genetic behavior of the F_1 hybrid and advanced generations derived from it. This work is being augmented by analyses of inter- and intraspecific variability as determined from morphology, bio-

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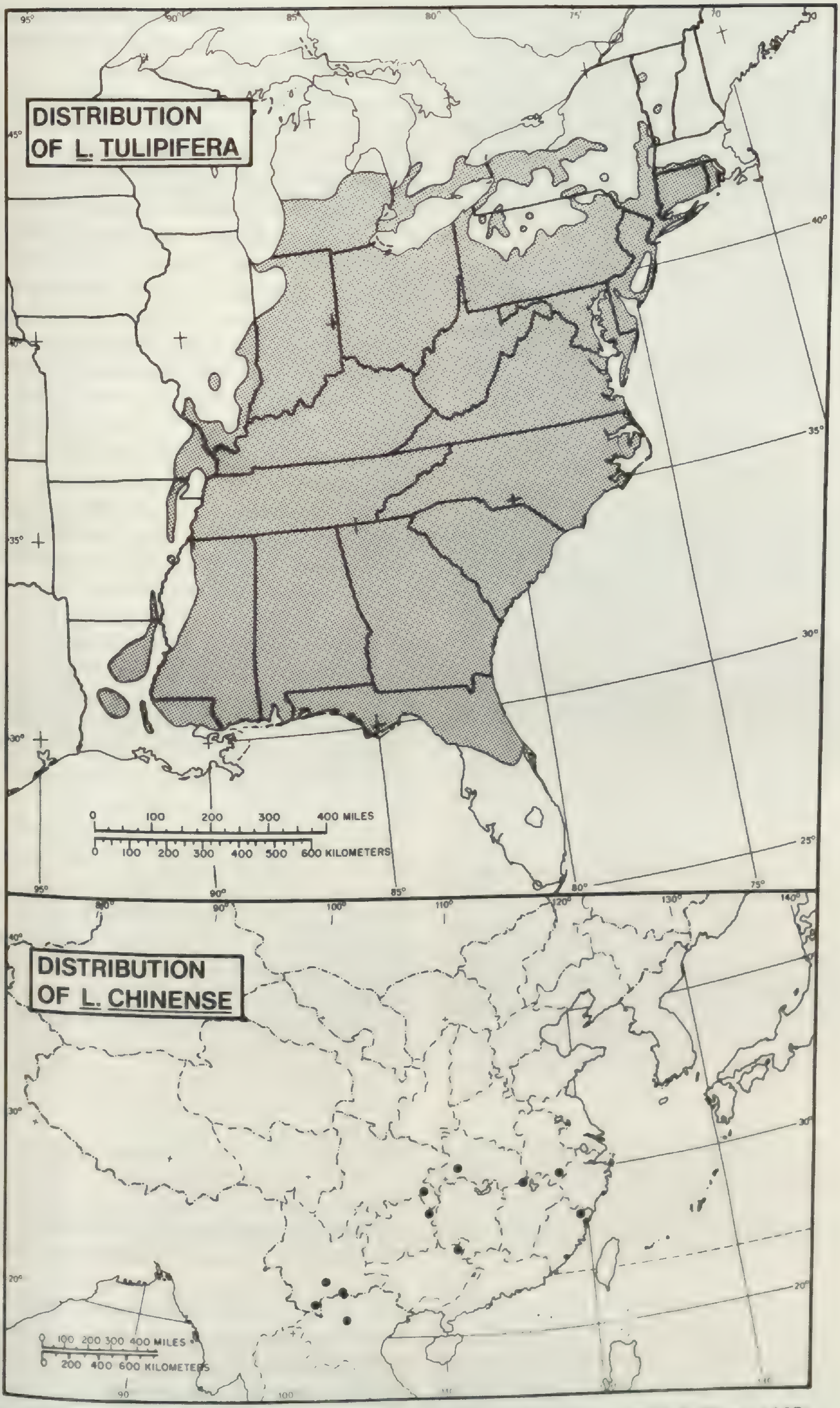

FIGURE 1. Distribution maps of *L. tulipifera* (Little, 1971) and *L. chinense* (Wu & Wang, 1957).

chemistry, and paleobotany. Our goal is to determine the amount of genetic divergence that has taken place in the genus *Liriodendron* and to gain insight into the evolution of divergence in a pair of long isolated species. In this report we will concern ourselves primarily with the results of the hybridization study.

MATERIALS AND METHODS

Plant materials. Seven accessions of *Liriodendron chinense* were available for this study. Six of these originated in 1948 from the Lushan Botanic Garden, Kuikiang, Kiangsi Province, China, by way of the Cabot Foundation and the Arnold Arboretum of Harvard University. Of these, five are maintained at the Blandy Experimental Farm, University of Virginia, Boyce, Virginia, and one is located in the Coker Arboretum on the University of North Carolina campus, Chapel Hill. The seventh *L. chinense* accession originated from a botanical garden in Hupei Province, China (A. R. Kruckeberg, pers. comm.) and was obtained from the MsK Nursery of Seattle, Washington. Individuals of *L. tulipifera* used in the crosses were native trees growing on or near the campus of the University of North Carolina.

Crossing experiments and progeny maintenance. Interspecific crosses between *Liriodendron tulipifera* and *L. chinense* were made in 1973 and 1977. The single tree of *L. chinense* in the Coker Arboretum was used as a male parent because it produced only a few, mostly inaccessible, flowers. Hand pollinations were made by applying pollen to the stigmas of buds emasculated one or two days prior to opening of the perianth. After pollen application, the buds were covered with paper bags for about two weeks to prevent pollen contamination. Self-pollinations were made by opening buds at the same stage, pollinating with pollen from the same tree and covering with bags as with the cross-pollinations. In the autumn fruits were harvested and stratified for at least 10 weeks at 4°C. They were sown in flats in the greenhouse, and seedlings were transplanted to 4-inch pots when they had reached the appropriate size. The saplings from the 1973 pollinations were planted in an alluvial field in the spring and summer of 1975. Individuals were spaced every six feet in rows ten feet apart. Weeds were partially controlled, but irrigation was not available. Seedlings from the 1977 group were treated initially as the earlier group, but were container grown under uniform conditions until 1980 when they were planted in the nursery at a site adjacent to the earlier group.

Biomass measurements. Relative biomass was estimated by parabolic volume of boles ($pv = 0.5\pi r^2h$, where r = radius and h = height) calculated from measurements made of the 1973 progeny in July 1982, and measurements made of the 1977 progeny in November 1979.

High pressure liquid chromatography (HPLC). Flavonoids were separated using HPLC. Dried leaves collected in late summer and early autumn were extracted in absolute methanol (0.5 g/5 ml), filtered to 0.45 μm and used for analysis without further treatment. A Waters Associates HPLC (6000A solvent delivery system, U6K injector, and 4500 variable wavelength injector) was used. An 8–15 μl sample was injected onto a 1.4 mm × 30 cm Ultrasphere-ODS column (5 μm particle size, reverse phase). Separation was obtained using a mobile phase of tetrahydrofuran : 2% acetic acid (22:78) at a flow rate of 1.0 ml/min (2,800 psi), an isocratic modification of gradient techniques used by Asen (1977) and Smith (1980). Detection was accomplished at 340 nm and 0.1 AUFS. Retention times and compound quantities were recorded on a Perkin-Elmer Sigma 10. Components were identified by co-chromatography with standards or spectral examination.

Electrophoresis and enzyme detection. Starch gel electrophoresis was performed on extracts from mature leaves. The methods of enzyme extraction, gel and electrode buffer compositions, and electrophoresis procedures followed or were slightly modified from Wendel and Parks (1982). Subsequent to electrophoresis, gels were sliced and stained for 16 enzyme systems (Table 5), according to methods published in Baum and Scandelios (1979), Cardy et al. (1980), Shaw and Prasad (1970), Siciliano and Shaw (1976), or Wendel and Parks (1982).

RESULTS

Crossing experiments. Interspecific hybrids of *Liriodendron* showed vegetative heterosis from early seedling stages. The heterotic response was in both the rate of growth and in the size of vegetative parts. The interspecific hybrids showed the typical bronze coloration of new foliage that characterizes the paternal parent, *L. chinense*, but is never seen in *L. tulipifera*. Two-way chromatographic separations of flavonoid extractives

TABLE 1. Seed set and survival from hybridizations between *Liriodendron chinense* and *L. tulipifera.*

	1973 Pollinations (field grown)			1977 Pollinations (container grown)			
	Self-Pollinations *L. tulip.*	*L. tulip.* × *L. tulip.*	*L. tulip.* × *L. chin.*	Self-Pollinations *L. tulip.*	Open-Pollinations *L. tulip.*	*L. tulip.* × *L. tulip.*	*L. tulip.* × *L. chin.*
Samaraceta harvested	5	7	15	11	38	14	12
Seeds germinated	11	127	273	19	138	231	230
Number germinated per samaracetum	2.2	18.1	18.2	1.7	3.6	16.5	19.2
Number surviving	Feb. 77 5	Feb. 77 64	Feb. 77 172	Nov. 79 8	Nov. 79 100	Nov. 79 132	Nov. 79 166
Percent survival	45	50	63	42	72	57	72

developed from a sample of hybrid trees showed essentially a full complementation of flavonoid extractives characteristic of the two parent species, as has also been reported by Santamour (1972). The heterotic response was so conspicuous by 1977 that we repeated the crosses with different parent trees of *L. tulipifera* to make certain that the growth response was not an artifact of unusually high specific combining ability of trees used in the original crosses.

Data on the germination and early survival of seedling progenies from the two hybridization series are summarized in Table 1. In *Liriodendron* samaras with fertile seeds cannot be readily distinguished from sterile samaras. Because all samaras of both types were planted, germination per fruit aggregate (samaracetum) rather than percent germination was recorded. In both years interspecific combinations resulted in as many or more seeds per aggregate germinated (18.2 and 19.2 versus 18.1 and 16.5 for the two years, respectively) than intraspecific combinations, and the percent survival was greater for the interspecific class of seedlings (63 and 72 versus 50 and 57). The number of viable seeds produced by the self-pollinations was very small. Most that germinated died in the seedling stages; however, two still survive from the first group of crosses. These are healthy trees only a little smaller than the average for trees of the same age derived from crosses between different *L. tulipifera* parents.

To add an additional comparison, open-pollinated fruits were collected from each of the parent trees used in the 1977 pollinations. Germination was very low (3.6 seedlings per aggregate) but the seedlings obtained showed good vigor and survivorship. Since some open-pollinated fruit aggregates produced several seedlings, whereas others produced few or none, we suspect that in the spring of 1977 inadequate cross-pollination was the rule for the *L. tulipifera* parents. In 1973 and 1977 open-pollinated fruits were collected from *L. chinense,* but a total of only three seedlings was obtained. [Open-pollinated seeds of *L. chinense* from Kuling, China had viability approximately equal to that of open-pollinated *L. tulipifera* in America (Johnson, 1948).] Since leaf extracts from the three open-pollinated *L. chinense* seedlings have flavonoid and isozyme profiles typical of the synthetic interspecific hybrids, *L. chinense* produced no seedlings through self-pollination.

As a measure of vegetative heterosis, biomass (bole volume) was calculated for both progenies (Tables 2 and 3). In all cases for the 1973 progeny, biomass was significantly greater ($P < 0.05$) for interspecific trees than for trees resulting from intraspecific crosses. The 1977 crossing series was designed to test whether the heterosis observed in the first series could be repeated. Different *L. tulipifera* parent trees were used, and an attempt was made to equalize the number of crosses in

TABLE 2. 1982 biomass of *Liriodendron* progenies synthesized in 1973.

Cross	Number of Progeny	Biomass[a] in m^3
L. tulipifera (Saunders tree[b]) × *L. chinense*	46	0.108[c]
L. tulipifera (Murphy tree[b]) × *L. chinense*	93	0.095[c]
L. tulipifera (Saunders tree) × *L. tulipifera* (Murphy tree)	53	0.074

[a] Biomass: $PV = 0.5\pi r^2 h$.
[b] Large individual parent trees of *L. tulipifera* on the University of North Carolina campus.
[c] Difference between interspecific and intraspecific hybrids significant at the 0.05 level.

TABLE 3. 1979 biomass of *Liriodendron* progenies synthesized in 1977.

Progeny	Number of Indi-viduals	Biomass in cm^3
Liriodendron tulipifera × *L. chinense* (3 different *L. tulipifera* parents)	164	19.23[a]
L. tulipifera self-pollinations	10	5.38
L. tulipifera open-pollinations	103	13.10
L. tulipifera × *L. tulipifera* (4 trees involved in 5 different combinations)	134	9.25

[a] Significantly different from all other progenies at the 0.001 level.

all combinations. Nearly all pollinated flowers produced fruits, but many were destroyed by squirrels. Table 3 is a summary of measurements made of the products of this second series of crosses. The interspecific hybrids had significantly greater biomass ($P < 0.001$) than the intraspecific hybrids or the open-pollinated group. The progeny of certain *L. tulipifera* parent trees consistently showed a greater heterotic response than others with respect to both inter- and intraspecific crosses, but this specific combining ability response did not obscure the rather great vegetative heterosis observed in the interspecific hybrids.

In the spring of 1981 several flowers were produced on a few of the interspecific and the intraspecific hybrid trees generated by the 1973 crosses. The flowers of the *Liriodendron tulipifera* × *L. chinense* hybrid were, like the leaves, somewhat larger than those of either parent species. Furthermore, orange pigment was present on most of the outer petal surface in flowers of the interspecific hybrid rather than being restricted to a narrow band toward the insertion of the petals as is typical of *L. tulipifera*. All available open-pollinated samaras from both the intra- and interspecific hybrid groups (a majority from the intraspecific hybrids) were planted in order to compare growth characteristics of the F_2 progenies. Four F_2 seedlings were obtained from the *L. tulipifera* × *L. chinense* hybrids, whereas about 40 seedlings were obtained from the hybrids between two *L. tulipifera* parents. The vigor and variability of both groups are about the same, and the F_2 seedlings from both groups appear indistinguishable.

Flavonoid and enzyme analysis. Leaf extracts from thirty populations (average of five trees each) of *Liriodendron tulipifera* and from the seven available trees of *L. chinense* were examined by high pressure liquid chromatography (HPLC). Fourteen probable, and four known, flavonoids (absorbent at 340 nm) from the *L. tulipifera* extracts were quantitatively assayed. All accessions of *L. tulipifera* were qualitatively alike in flavonoid makeup, but large quantitative differences were common. These quantitative differences are large enough to appear as qualitative differences on thin-layer or paper chromatographic separations of crude extracts. Small, but measurable quantitative differences were characteristic of wild trees from the same locality (population), while major quantitative differences often occurred between closely spaced populations. Inspection of the quantitative data (Table 4) for the 30 populations provided no obvious correlation with altitude or geographical location. Furthermore, principal component analysis of these data failed to reveal any obvious clustering of populations nor were there any significant correlations obtained between population positions along the first two principal components and altitude, latitude or longitude.

The flavonoid extractives from the five *Liriodendron chinense* trees from the Blandy Experimental Farm were very similar to each other, whereas the tree from the Coker Arboretum differed only slightly from them. In general the six trees are at least as similar to each other as trees

TABLE 4. Distribution of 340 nm absorbent extractives in 30 populations of *L. tulipifera*.

Population #	Location	Flavonoid and Flavonoid-like Extractives[a]																	
		1	2	3	4	5	6	7	8	9[b]	10	11	12[c]	13[d]	14	15[e]	16	17	18
1	Macon Co., NC	2.3	27.4	9.0	2.6	3.8	—	0.9	12.6	14.0	5.3	3.8	6.5	2.0	—	1.7	1.4	2.2	0.6
5	Rabun Co., GA	—	49.2	2.1	0.7	5.9	1.6	2.4	26.9	10.0	—	0.6	1.8	2.0	0.3	0.3	0.3	0.4	1.3
8	Transylvania Co., NC	—	32.3	11.0	4.5	4.7	3.2	2.9	0	6.8	0.5	1.5	4.4	2.2	—	0.2	1.3	4.0	0.9
10	Transylvania Co., NC	4.9	5.6	4.7	0.7	0.4	0.6	2.0	9.7	7.7	2.2	0.5	16.0	1.1	—	—	1.8	—	0.3
12	Macon Co., NC	—	36.4	0.2	1.9	3.8	0.7	0.9	28.0	12.2	2.0	1.6	3.7	1.8	0.2	0.5	0.4	0.7	1.1
16	Transylvania Co., NC	1.8	18.0	2.7	0.7	1.1	0.6	3.4	16.9	25.7	5.8	2.5	9.0	5.2	—	1.2	0.2	1.7	0.4
17	Henderson Co., NC	—	40.4	0.5	1.4	4.5	0.9	1.5	16.0	8.8	2.7	1.6	2.8	2.2	—	2.4	—	2.9	1.9
19	McDowell Co., NC	3.8	22.7	6.8	3.1	3.2	0.6	1.1	26.9	15.0	0.3	1.7	3.7	3.1	0.2	1.1	1.2	2.3	0.9
25	Swain Co., NC	—	31.4	10.1	3.9	5.3	0.9	0.3	1.0	15.9	4.1	3.0	4.5	2.0	0.3	0.9	1.1	1.5	0.9
28	Graham Co., NC	0.9	21.6	2.1	1.0	3.1	0.9	1.4	40.0	14.9	—	1.8	3.2	2.0	0.1	0.7	0.9	1.5	0.8
31	Graham Co., NC	—	25.2	3.4	2.4	2.3	0.4	0.2	27.8	12.2	2.8	1.7	3.5	2.7	0.5	0.8	0.7	1.1	0.8
32	Swain Co., NC	2.1	29.9	4.7	—	1.6	2.2	2.3	42.7	5.0	—	1.3	4.4	2.1	0.1	1.0	0.5	0.7	0.7
33	Macon Co., NC	5.8	34.0	—	0.1	3.7	2.5	2.8	25.8	10.0	0.3	1.5	2.1	1.9	0.1	0.4	0.4	1.7	0.6
41	Transylvania Co., NC	3.3	39.8	—	0.2	2.8	1.9	3.5	25.0	6.9	4.1	1.3	1.0	2.6	0.1	0.2	0.3	0.5	0.6
44	Macon Co., NC	—	38.3	9.6	2.5	3.8	2.5	2.4	4.0	21.4	—	1.0	3.8	2.6	0.1	—	0.8	2.4	1.8
46	Buncombe Co., NC	5.9	29.9	12.3	1.6	2.2	—	3.4	4.0	16.9	6.0	1.4	3.9	3.9	1.2	1.6	1.8	3.9	1.1
47	Buncombe Co., NC	4.7	26.7	4.5	2.2	3.2	1.5	2.5	16.0	16.0	2.4	0.8	4.0	3.5	0.1	0.7	—	1.2	0.7
55	Davidson Co., NC	—	49.9	—	3.4	13.3	2.0	2.7	0.3	2.1	1.1	—	2.4	2.2	—	—	—	—	2.6
57	Orange Co., NC	1.7	27.5	10.7	1.9	2.8	—	2.5	5.0	25.7	5.9	3.0	7.1	1.9	—	1.1	2.5	3.1	1.3
58	Stokes Co., NC	—	36.2	7.0	4.5	4.9	1.7	1.6	1.1	7.1	2.4	3.1	5.6	1.7	0.5	0.8	1.1	2.6	1.1
63	Jackson Co., NC	—	36.6	1.7	0.6	2.2	0.3	1.0	44.7	5.0	0.8	1.4	2.8	1.6	0.5	0.5	0.5	0.4	1.3
69	Avery Co., NC	4.3	28.9	9.4	4.0	2.2	1.0	1.2	4.0	16.8	3.1	3.0	4.9	2.8	0.8	1.1	1.6	2.9	1.1
71	Alleghany Co., NC	—	36.1	—	0.3	5.1	2.3	3.1	30.0	10.0	2.0	0.9	3.1	3.0	0.4	0.4	0.2	0.8	0.7
73	Floyd Co., VA	—	38.2	5.4	3.0	3.0	0.9	0.9	11.8	14.9	—	1.2	5.1	2.7	—	0.8	2.8	3.8	1.6
79	Greene Co., VA	3.5	36.2	7.0	1.2	8.2	—	2.0	3.0	15.0	4.3	0.8	4.6	3.0	—	2.1	1.3	3.6	1.9
83	Perry Co., PA	3.8	18.1	4.2	1.2	4.4	—	3.0	15.0	15.0	9.0	1.9	8.7	5.4	—	2.1	—	1.2	0.8
84	Snyder Co., PA	—	28.8	9.3	3.3	3.5	3.7	2.0	1.0	8.0	—	0.7	13.8	3.9	—	2.9	2.9	13.1	0.7
89	Lycoming Co., PA	—	35.3	10.5	4.3	3.8	1.6	2.6	12.0	10.0	—	0.5	1.5	2.9	0.1	2.5	2.6	4.4	1.7
82A	Watauga Co., NC	—	18.5	1.2	0.4	0.7	—	1.5	17.2	21.8	6.4	4.8	7.8	9.7	0.8	1.9	0.9	2.0	0.2
82B	Montgomery Co., VA	0.1	19.3	2.7	—	1.9	—	1.7	35.0	15.0	4.7	2.1	6.3	6.8	0.3	2.1	—	1.4	0.3

[a] Values indicate % of total extract.
[b] Quercetin-3-rutinoside.
[c] Kaempferol-3-rutinoside.
[d] Quercetin-3-glucoside.
[e] Kaempferol-3-glucoside.

TABLE 5. Enzymes resolved from *Liriodendron* leaves.

Alcohol dehydrogenase
Aldolase
Aspartate aminotransferase
Catalase
Diaphorase
Fluorescent esterase
Glutamate dehydrogenase
Glyceraldehyde-3-phosphate dehydrogenase
Isocitrate dehydrogenase
Malate dehydrogenase
Peroxidase
Phosphoglucose isomerase
Phosphoglucomutase
Superoxide dismutase
Shikimic acid dehydrogenase
Triose phosphate isomerase

of any single *L. tulipifera* stand. The seventh tree, from the MsK Nursery, is very different in its flavonoid pattern in comparison to the other six trees of *L. chinense*. The differences in flavonoid composition between the two accessions of *L. chinense* from divergent parts of China are at least as great as the maximum difference in flavonoids observed between different wild populations of *L. tulipifera*.

Sixteen enzyme systems were resolved in a survey of *Liriodendron* leaf extracts (Table 5). While it is uncertain how many genetic loci encode these systems, reasonable estimates can be obtained based upon the patterns of variation observed in the sampled material and upon a knowledge of the quaternary structure of each enzyme. Crossing experiments designed to document the genetic control of the resolved systems have been initiated, and the results of these experiments will be reported elsewhere (Wendel & Parks, unpub.). A preliminary assessment of allozyme variability revealed a sharp contrast in the degree of observed heterozygosity for the two species. While approximately 15 percent of the loci were heterozygous in a sample of three populations of *L. tulipifera*, not a single heterozygote has been observed in any of the seven *L. chinense* specimens examined. Six of these specimens (the Coker and the Blandy trees) were allozymically identical, whereas the seventh (the MsK tree) was very different. This last tree was apparently equally homozygous, but for alleles different than those of the other six trees at a number of loci.

DISCUSSION

Despite a strong tendency for parthenocarpy (Stairs & Wilcox, 1966; pers. obs.), *Liriodendron* trees of either species set few viable samaras without cross-pollination; however, there is a low, but measurable, self-fertility in *L. tulipifera* (Table 1; Taft, 1966). It is thought that a large amount of self-pollination under natural conditions is the major cause of poor samara viability in *Liriodendron* (Guard, 1943; Santamour, 1972; Taft, 1966). In a number of studies (Guard, 1943; Santamour, 1972; Stairs & Wilcox, 1966; Taft, 1966) of *L. tulipifera*, controlled cross-pollination has very substantially increased the number of viable samaras per samaracetum. Similar mechanisms may be operating in *L. chinense*. Santamour (1972) recorded good seed set for *L. chinense* at the Blandy Experimental Farm, where tulip trees of both species are planted relatively close together. Our specimen of *L. chinense* at the Coker Arboretum, however, was isolated from all other individuals of *Liriodendron*, and we have obtained only three viable seeds from numerous samaraceta collected in two seasons.

Vegetative heterosis of the juvenile interspecific hybrid between *Liriodendron tulipifera* × *L. chinense* has also been observed in the United States by Santamour (1972) and in China by He (pers. comm.). The rapid growth rate has not diminished in trees that have reached reproductive age in any of the plantings. Intraspecific vegetative heterosis has been observed in *L. tulipifera* (Stairs, 1968; Stairs & Wilcox, 1966; Taft, 1966), but the increment of increase is not as great as that of the interspecific hybrid.

The production of vigorous F_1 progenies from crosses between different species of the same genus of woody plants is not in itself unusual or highly significant. Grant (1971) named the kind of interspecific interfertility found in many woody plant genera the "*Ceanothus* pattern." This pattern is typified by *Magnolia*, in which there are few barriers to crosses between species of the same subgenus, despite their great geographical and temporal isolation, but a complete block to the successful hybridization of species belonging to the two different subgenera (Spongberg, 1976; Treseder, 1978). Because these hybrids have been made and used for horticultural purposes, there is little information about the fertility of the hybrids.

In woody plants successful crosses have been made, or reported, between various American,

European, or Asian species of *Abies* (Rohmeder, 1961), *Aesculus* (*A.* × *carnea* Hayne; Upcott, 1936), *Betula* (Johnson, 1939; Smith & Nichols, 1941), *Campsis* (*C.* × *tagliabuana* (Vis.) Rehder; Sax, 1933), *Castanea* (Johnson, 1939), *Catalpa* (*C.* × *hybrida* Hort. ex F. L. Späth; Smith, 1941), *Juglans* (Johnson, 1939), *Larix* (*L. eurolepis* Henry; Sax, 1932; Smith, 1941), *Liquidambar* (He & Santamour, pers. comm.), *Pinus* (Mirov, 1967), *Platanus* (*P.* × *acerifolia* (Ait.) Willd.; Sax, 1933), *Populus* (Johnson, 1939, 1942, 1946), *Quercus* (Johnson, 1939), and *Taxus* (Johnson, 1939).

Hybrid fertility and F_2 vigor and variability are better indicators of species relationships in most woody plant genera than the mere fact of species compatibility. In five of these genera (*Campsis, Castanea, Catalpa, Platanus,* and *Populus*) the authors reported F_1 fertility and the production of an F_2 generation. Sax (1932) reported that the *Larix* hybrid had essentially normal cytological behavior in the F_1; however, an F_2 generation was not grown. The *Aesculus* hybrid, *A.* × *carnea,* was shown by Upcott (1936) to be a spontaneous allotetraploid with reduced F_1 fertility.

In the other studies of hybridization of *Liriodendron tulipifera* and *L. chinense* (Santamour, 1972; and those made by Prof. Y. Peitzung at the Nanjing Botanical Garden in 1963 and 1965, *fide* correspondence with Prof. T. T. Yü, Academia Sinica, Beijing, China) F_2 data have not yet been generated. Our results from the small F_2 seed crop harvested in 1981 lead us to suspect that such hybrids will show considerable fertility and produce a relatively vigorous F_2 population. The high level of heterosis observed in our *Liriodendron* hybrids coupled with the suggestion of hybrid fertility indicates that the Chinese and American species of *Liriodendron* have not diverged very far genetically despite long separation in time and space. This conclusion is currently being further evaluated: In the spring of 1982 a much larger number of flowers was produced on our F_1 plants, and reciprocal sibling F_2 crosses and backcrosses to *L. tulipifera* were made. (Unfortunately, no reproductive plants of *L. chinense* were available at that time.) Fruits from these crosses have been harvested, and a report on their germination and growth will appear at a later date.

In terms of their geographical ranges, the two species of *Liriodendron* cover similar total areas. However, *L. tulipifera* is a common and abundant plant throughout much of the southeastern United States, whereas *L. chinense* is limited to a small number of individuals in several widely separated populations (Shan-an He, Jiangsu Institute of Botany, Nanjing, China, pers. comm.; Fig. 1). Individuals of *L. chinense* have a low degree of vigor (pers. comm.) which approximates that of our inbred *L. tulipifera* (one generation). Our very limited isozyme and flavonoid data on *L. chinense* indicate that these small populations have become genetically divergent, most likely as a result of drift. We suggest that the small number of extant trees of *L. chinense* suffer to some degree from inbreeding depression, a premise supported by the complete absence of isozyme heterozygosity. If this hypothesis is indeed true, hybrids between individuals from different populations should be markedly heterotic. It is our intention to expand the study of variability between and within *L. tulipifera* and *L. chinense* in collaboration with Chinese botanists.

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BIOGEOGRAPHIC, TAXONOMIC, AND CLADISTIC RELATIONSHIPS BETWEEN EAST ASIATIC AND NORTH AMERICAN *CRATAEGUS*[1]

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Abstract

The genus *Crataegus* possesses some 150 species, more or less, according to how apomictic complexes are treated. Two of the largest series: *Oxyacanthae* (mainly European, of about 25 species) and *Azaroli* (Mediterranean to Central Asiatic, of about 12 species) do not at first sight impinge on the topic of this paper, but their cladistic significance indicates otherwise. In temperate Asia east of about 75°E long. (through Tibet) there are some 15 species of *Crataegus* in various sections, none of which occur in North America, unless *C. scabrifolia* of Yunnan be aligned in a North American section. In North America some 100 species might be recognized in about 20 series or sections, some of which, e.g. *Cordatae*, are very distinct, one of which, *Apiifoliae*, is very similar to European *Oxyacanthae*, and another of which (sect. *Mexicanae*) is extremely like Chinese *C. scabrifolia*. Most other North American species represent a heterogeneous collection of more or less closely allied series with some apparent affinities to the *Sanguineae* of northern Asia or the Chinese and Japanese species. Cladistic analysis, using extensive outgroup comparison with other maloid genera, indicates *C. scabrifolia* (Yunnan) and *C. mexicana* to be not only among the most primitive, but also mutually similar. Their affinity with *Pyracantha* and that of other *Crataegus* with *Mespilus* indicates basal possibilities for the genus. One is thus led to postulate a primitive scabrifolioid-mexicanoid stock of warm-temperate origin that was able to cross Beringia in the early Tertiary or Miocene and migrate southward. Thence, evolution toward the extant species is most parsimoniously derived from a south China relictual base with spread into western Eurasia (one major line); eastern Asia through Beringia to a North American diversification (a minor line); and a minor North American diversification from mexicanoid stock. It should be noted that (except for modern introductions) no *Crataegus* species of North America and Eastern Asia are conspecific. Also, except for the postulated ancient relicts, no two species from the two continents are even particularly close taxonomically. The evidence suggests that *Crataegus* is an old genus, quite possibly of early Tertiary age, that spread once or twice into the Americas with two probable major diversifications and probable much late Tertiary extinction. Present-day Eurasian *Crataegus* are mainly derived from Chinese stock. Thus, while the Tertiary period permitted somewhat parallel evolution of Asian and North American *Crataegus*, except for relictual taxa, they are not very closely related.

When I was deciding what materials on the enormously fascinating and complex genus *Crataegus* might be presented for the St. Louis Systematics Symposium in 1982 I had to come to terms with how to handle incomplete work. My answer was strongly influenced by the view that *Crataegus* has received no comprehensive treatment that was both modern and effective. Therefore, this contribution, which incorporates modern findings of other workers in addition to my own, represents more than a progress report—it sets out an entire scenario. I feel, therefore, that it is no exaggeration to claim that the progress made in the systematics of *Crataegus* in recent years permits one to present a credible biogeographic analysis of the genus for the first time. This progress has included modern, floristic works for almost the whole of the range of the genus, numerous studies on reproductive biology, e.g. introgressive situations (e.g. Byatt, 1975, 1976a; Love & Feigen, 1979), chromosome counts showing three levels of ploidy (2x, 3x, 4x) (Gladkova, 1968; Muniyamma & Phipps, 1979a; Dickinson, unpubl.; Smith, unpubl.), the cytological proof of apomixis (Muniyamma & Phipps, 1979b) and the extension of this knowledge to a number of taxa (Muniyamma & Phipps, 1984; Dickinson & Phipps, submitted; Smith & Phipps, unpubl.), knowledge of the phenetic dissection of apomictic complexes (Sinnott & Phipps, 1983; Dickinson & Phipps, submitted; Smith & Phipps, unpubl.), etc. The specific contributions of this paper will include a numerical taxonomic analysis of the genus that permits of more rational

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TABLE 1. J. C. Loudon's Classification of *Crataegus* in Arboretum et Fruiticetum Brittanicum (1838).

I.	Sect. *Coccineae* Loud. (p. 816) 2 species, incl. *C. coccinea* L. both with varieties
II.	Sect. *Punctatae* Loud. (p. 818) 2 species, incl. *C. punctata* Ait. (sic)
III.	Sect. *Macracanthae* Loud. (p. 819) 1 species: *C. macracantha* Lodd.
IV.	Sect. *Crus-galli* Loud. (p. 820) 3 species, incl. *C. crus-galli* L.
V.	Sect. *Nigrae* Loud. (p. 822) 2 species: *C. nigra* Waldst. & Kit. and *C. purpurea* Bosc.
VI.	Sect. *Douglasii* Loud. (p. 823) 1 species: *C. douglasii* Lindl.
VII.	Sect. *Flavae* Loud. (p. 823) 3 species, incl. *C. flava* Ait.
VIII.	Sect. *Apiifoliae* Loud. (p. 824) 1 species: *C. apiifolia* Michx. (= *C. marshallii* Egglest.)
IX.	Sect. *Microcarpae* Loud. (p. 825) 2 species: *C. spathulata* Ell. (sic) and *C. cordata* L.f.
X.	Sect. *Azaroli* Loud. (p. 826) 5 species, incl. *C. azarolus* L.
XI.	Sect. *Heterophylla* Loud. (p. 829) 1 species: *C. heterophylla* Flugge
XII.	Sect. *Oxyacantha* Loud. (p. 829) 1 species: *C. oxyacantha* L. [= *C. laevigata* (Poir.) DC.]
XIII.	Sect. *Parvifoliae* Loud. (p. 841) 3 species, incl. *C. parvifolia* Ait. (= *C. uniflora* Muenchh.)
XIV.	Sect. *Mexicana* Loud. (p. 843) 1 species: *C. mexicana* Moc. & Sessé
XV.	Two other sections are not now included in *Crataegus*

species groupings on a world-wide basis than hitherto presented, the biogeographic analysis itself, and supportive interpretations from cladistics, dispersal biology, and to a lesser extent, considerations of paleoclimate, paleogeography and some *Crataegus* fossil evidence. It is my considered view that such a synthesis of mutually supportive data from these different viewpoints and workers is vital to disentangling a genus such as *Crataegus*, which has been called somewhat alarmingly "a veritable witches' brew."

The conditions for generating an adequate biogeographical analysis are: (a) an adequate species-list; (b) adequate range maps; (c) understanding of species' relationships within the taxa under study; (d) knowledge of dispersal biology, and (e) knowledge of these topics in times past. I consider that (a) and (b) exist to adequate standards from literature compilation, a revision of our own (Phipps & Muniyamma, 1980) and herbarium studies on many species. I will present new materials for (c) in this paper (phenetic and cladistic) and will use available knowledge on (d) and (e). The understanding of the dispersal biology of *Crataegus*, although sketchy, appears reliable for the arguments to be made, although paleontological data, excepting pertinent paleogeography, is sparse.

The genus *Crataegus* is taxonomically quite well-known at the regional level, although apomictic complexes, some active introgressive situations, and some relatively rare segregates from apparently older hybrid situations may complicate the picture locally. The genus is most common between 30° and 50° N latitude although some extensions north and south of these limits may be found. In spite of the abundance of species and the ecological significance of *Crataegus*, there is no really worthwhile and comprehensive treatment of this genus that has been presented hitherto. Regional floras, e.g. Franco (1968), for Europe, Maire (1980) for North Africa, Browicz (1972) for Turkey, Riedl (1969) for the Flora Iranica region, Pojarkova (1939) for the USSR, and Yü and Ku (1974) for China cover Eurasia effectively at the normal level of good floristic treatments. The remaining smaller areas in Asia possessing *Crataegus* (Levant, Korea, Japan) are also adequately covered. The floristic effort in North America has been just as great with major contributions by Palmer (e.g. 1953) and Kruschke (1965) for the Northeast and Tidestrom (1933) for the Southeast. State and regional floras for the United States west of the Mississippi, Canada, and Alaska, combine to cover all species of the western half of the United States and Canada but there is no comprehensive treatment for Mexico since Standley (1922). However, in spite of apparently complete regional coverage, there remains uncertainty about the reliability of treatments of certain species groups, especially some of those concentrated in Texas and the eastern United States. The situation undoubtedly reflects real taxonomic problems, as is now demonstrated, for instance, by the work on cytology and reproductive behaviour, on apomixis, on polyploidy, on phenetic dissection in the genus, as mentioned earlier, and is thus not an artefact of bad taxonomy. Thus, the taxonomic problems are real and almost certainly have contributed to the avoidance of a holistic study of the genus. These taxonomic difficulties can, of course, lead to some lack of precision for the biogeographical analysis because of the incommensurability of taxa of the 'same' rank and certain fuzzy species' boundaries based on taxonomic uncertainties

TABLE 2. C. K. Schneider's classification of *Crataegus* in Illustriertes Handbuch des Laubholzkunde (1906). Note—authorities as attributed by Schneider are not necessarily correct. Phipps (1983) provides correct citations for serial and sectional names.

1. Sect. *Pinnatifidae* Zabel (p. 769) 3 species, incl. *C. pinnatifida* Bunge
2. Sect. *Sanguineae* Zabel (p. 771) 6 species, incl. *C. sanguinea* Pallas
3. Sect. *Douglasianae* Rehd. (p. 775) 2 species, incl. *C. douglasii* Lindl.
4. Sect. *Tomentosae* Sarg. (p. 776) 3 species, incl. *C. tomentosa* L.
5. Sect. *Pentagynae* C. K. Schneid. (p. 777) 2 species: *C. pentagyna* Waldst. & Kit. and *C. nigra* Waldst. & Kit.
6. Sect. *Oxyacanthae* Zabel (p. 779) 5 species, incl. *C. oxyacantha* L.
7. Sect. *Orientales* Zabel (p. 786) 7 species, incl. *C. orientalis* Pallas
8. Sect. *Microcapae* Koch (p. 790) 3 species, incl. *C. apiifolia* Michx.
9. Sect. *Brevispinae* Beadle (p. 791) 2 species, incl. *C. brachyacantha* Engelm. & Sarg.
10. Sect. *Flavae* Sarg. (p. 792) 2 species, incl. *C. flava* Ait.
11. Sect. *Uniflorae* Beadle (p. 793) 1 species: *C. uniflora* Muenchh.
12. Sect. *Cuneatae* Rehd. (p. 793) 1 species: *C. cuneata* Sieb. & Zucc.
13. Sect. *Mexicanae,* sect. provis. (p. 794) 1 species: *C. stipulosa* Steud.
14. Sect. *Aestivales* Sarg. (p. 794) 1 species: *C. aestivalis* Torr. & Gr.
15. Sect. *Punctatae* Sarg. (p. 794) 2 species, incl. *C. punctata* Jacq.
16. Sect. *Crus-galli* Sarg. (p. 796) 1 species: *C. crus-galli* L.
17. Sect. *Triflorae* Beadle (p. 797) 1 species: *C. triflora* Chapm.
18. Sect. *Molles* Sarg. (p. 797) 2 species, incl. *C. mollis* Scheele
19. Sect. *Virides* Sarg. (p. 798) 2 species, incl. *C. viridis* L.
20. Sect. *Pruinosae* Sarg. (p. 798) 1 species: *C. pruinosa* K. Koch
21. Sect. *Coccineae* Sarg. (p. 799) 4 species, incl. *C. coccinea* L.
22. Sect. *Intricatae* Sarg. (p. 801) 3 species, incl. *C. intricata* Lange

TABLE 3. Series of the genus *Crataegus* as proposed by Rusanov (1965) in Dendrologii Uzbekistanii (from Cinovskis, 1971).

Ser. 1. *Pinnatifidae*	Ser. 14. *Macracanthae*
Ser. 2. *Henrianae* (sic)	Ser. 15. *Punctatae*
Ser. 3. *Microcarpae*	Ser. 16. *Rotundifoliae*
Ser. 4. *Oxyacanthae*	Ser. 17. *Intricatae*
Ser. 5. *Nigrae*	Ser. 18. *Brainerdianae*
Ser. 6. *Pentagynae*	Ser. 19. *Cordatae*
Ser. 7. *Douglasianae*	Ser. 20. *Silvicolae*
Ser. 8. *Sanguineae*	Ser. 21. *Pruinosae*
Ser. 9. *Calpodendra*	Ser. 22. *Molles*
Ser. 10. *Virides*	Ser. 23. *Dilatatae*
Ser. 11. *Cuneatae*	Ser. 24. *Coccineae*
Ser. 12. *Mexicanae*	Ser. 25. *Tenuifoliae*
Ser. 13. *Crus-galli*	

The state of current taxonomy may be briefly reviewed here. Loudon (1838) grouped *Crataegus* into 14 sections (Table 1) of similar species. In doing so, he presented the standard format for *Crataegus* classification that has persisted through, for instance, the work of C. K. Schneider (1906), whose classification is presented in Table 2, Sargent (1902, 1903), Palmer (1953), Kruschke (1965), Rehder (1940), Rusanov (1965—see Table 3), Cinovskis (1971), and others. These treatments vary in the geographical region covered, Kruschke and Palmer being North American, Pojarkova Russian, and the others world-wide. They also vary in the predominant rank used (Section, Series, 'natural group' or 'group'—German 'Gruppe') and the number of species known to and accepted by the author. But what these classifications have in common is "flatness." Neither Loudon's 14 sections nor Rusanov's 25 series claim any further hierarchical groupings or interrelationships. Thus, the established view of *Crataegus* taxonomy, that of many small species groups, represented the most that taxonomists would venture for some 140 years.

However, Cinovskis (1971: 19), in *Crataegi Baltici,* presented a remarkably complex reticulate set of interrelationships (Fig. 1) that, although possibly close to the botanists' dream of *Crataegus,* is very confusing and not scientifically very realistic. At the other extreme, El-Gazaar (1980) attempted to cut the Gordian Knot by erecting two sub-genera (Fig. 2), on the basis of differential leaf-shape, geographical distribution, and base chromosome number. Whereas sub-genus *Crataegus* represents, more or less, on his criteria, two related sections (*Oxyacanthae* and *Azaroli*) it is not, as he claims, restricted to Eurasia (note *C. marshallii* in the United States). His other group, "*Americanae,*" purports to represent the remainder of *Crataegus.* However, the remainder of *Crataegus* is much more variable

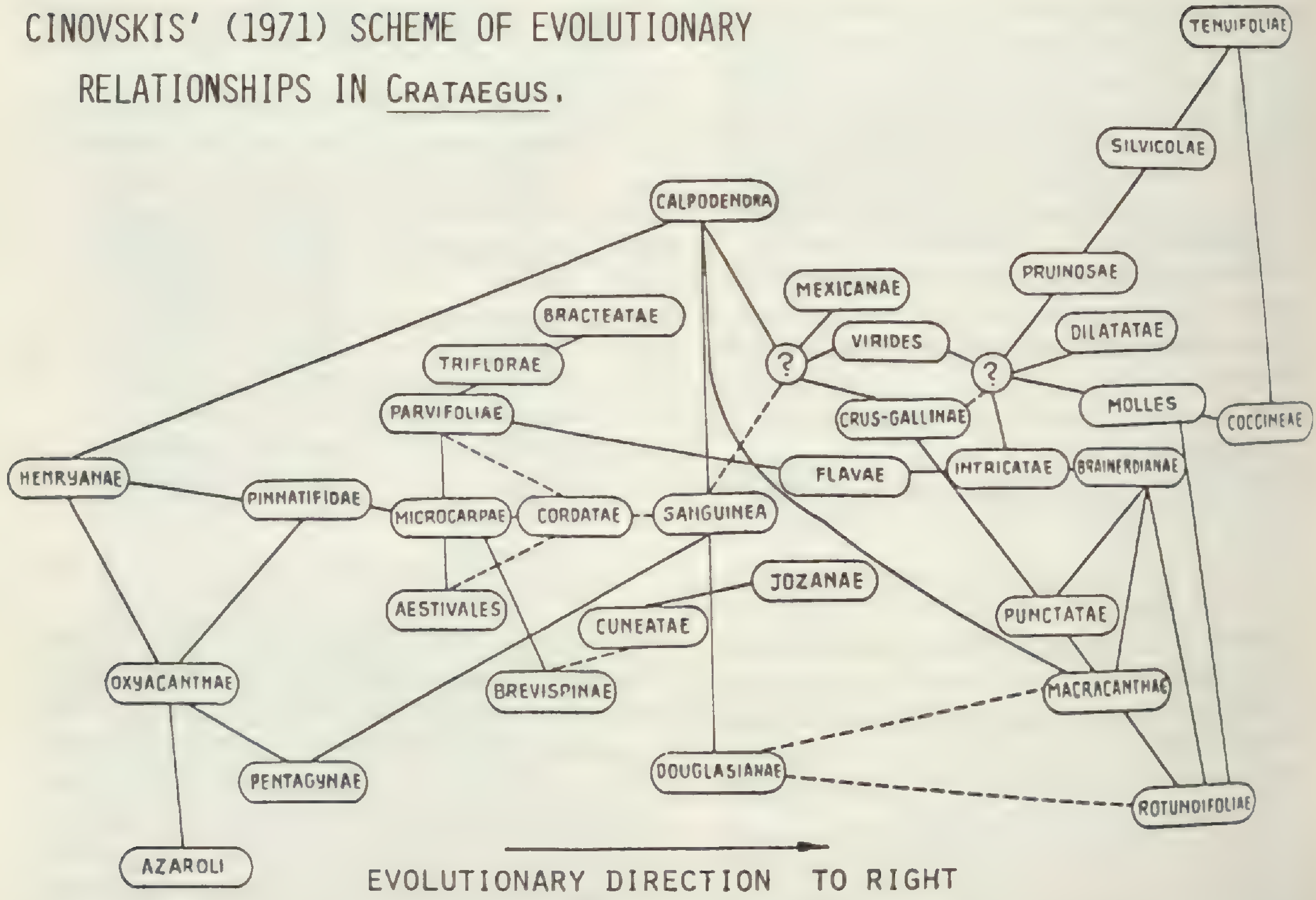


FIGURE 1. Cinovskis' (1971) scheme of evolutionary relationships in *Crataegus*.

in leaf morphology than this simple division implies, "*Americanae*"-type leaf morphology characterising most east Asian species whereas, in quoting Longley's (1924) paper based on hand-sectioned material, El-Gazaar and Badawi (1977) resurrected the totally discredited notion of x = 16 for North American species. El-Gazaar, regrettably, did little more than reinforce a notion already well understood by Sargent, Schneider, and others that a distinct "Oxyacanthoid" (small leaf, deeply lobed) leaf shape existed, and from there went on to totally misleading suppositions.

Thus, prior to the work to be presented here, no credible set of interrelationships within *Crataegus* has been proposed.

MATERIALS

Some 145 species of *Crataegus* are held to exist (Appendix A) and it is neither necessary nor convenient to use all for this study. For the numerical taxonomic work all the species groups (e.g. sections, series) were sampled in order to be certain to include all pertinent phenetic variation. This generated a list of 75 species (identified in Appendix A), some quite narrowly defined. This same set of species is also used for the cladistic study.

However, because of the title of the St. Louis Symposium, the suite of taxa used in the detailed biogeographic analysis for this paper excludes the 20–25 *Oxyacanthae* and the ten or so *Azaroli* of Western Asia, Europe, and North Africa and the few small sections unique to this region. The westward demarcation line for the study is 75°E longitude. The 62 taxa used in the biogeographic study include essentially all eastern Asian (*sensu* this paper) and North American *Crataegus*. Although using a relatively complete set for the biogeographical study, somewhat different taxonomic criteria from those used in defining the cladistic set have had to be used in selecting the operational taxonomic units (OTUs) to be used in some cases. Specifically, where range-limits are still uncertain among taxonomically very close species, an entire series was sometimes used as an OTU. The lack of consistency among taxonomic rank of OTUs might concern the nominalistically inclined, but in actual fact is unavoidable.

The choice of 75°E long. western limit for eastern Asia is somewhat arbitrary. However, this

EL-GAZAAR 1977, 1980

	subgenus *Crataegus*	subgenus *Americanae*
base chr. no.	$x = 17$	$x = 16$[1]
leaves	deeply incised[2]	shallowly lobed[3]
veins to sinuses	present	absent[3]
distribution	Eurasia	North America

[1] quoting Longley, 1924 who used hand-sectioned material—correct is $x = 17$ (Moffet '31, Gladkova '68, M & Ph '79).

[2] Some Eurasian species have subgenus *Crataegus* foliage type.

[3] Some N. American species have subgenus *Americanae* foliage type.

FIGURE 2. El-Gazaar's (1977, 1980) subdivision of *Crataegus* into two subgenera.

western study limit passing through the currently impenetrable central Asian massif of Xinjiang-Qinghai-Xijang both simultaneously and fortuitously proves to coincide with a natural taxonomic and biogeographic partition in *Crataegus*.

DATA

The morphological data used consist of 49 characters from habit, branch, thorn, leaf, inflorescence, flower, and fruit (Table 4). These are obvious *Crataegus* characters that any taxonomist would use except for the emphasis on thorn, which is underlined by this writer. All 49 characters were used for the phenetic studies. For the cladistic studies, those 18 characters that could, with adequate confidence, be polarised, were selected (Table 5). These were appropriately recoded (see later discussion).

The biogeographical data base consists of 62 range maps. Range maps made from locality coordinates (dot maps) of individual records are by far the most sensitive, because they possess the most information content (e.g. see Phipps, 1975a) for numerical biogeographic analysis. Range maps with smooth-curve edges and no internal detail were substituted, however, because not enough dot maps are available yet. There is no problem in creating quite accurate maps from the floras mentioned, supported by more local floras, so long as consistent taxonomic decisions are made in coordinating data from different sources and attention is paid to synonymy when grouping taxa, as discussed earlier.

PLAN OF WORK

A phenetic study using 49 morphometric characters was conducted to test what species groups existed in *Crataegus* worldwide. For this, 75 species were used, sampling all sections of the genus. The characters used are largely those conventional in *Crataegus* taxonomy, but leaf lobing and associated attributes, as emphasised already by Schneider (1906) and taken up again by El-Gazaar; and thorn type, as emphasised by this author (e.g. Phipps & Muniyamma, 1980) have more prominence than usually accorded by most workers. Due to the exceptionally large number of herbarium specimens available, median or modal values were scored. The OTUs were subjected to comparison by euclidean distance and clustered by minimum variance clustering to derive a phenogram, and to ordination by the dispersion coefficient and principal components analysis to derive a scattergram. An r-type components analysis indicated character loadings.

The biogeographical analysis depended on scoring presence-absence of species on an equiform grid of 640 km² laid on eastern Asia and North America (Figs. 3, 4). This method is somewhat crude because it does not optimize grid size

TABLE 4. Morphometric data for *Crataegus* study.

Habit:
1. tree through small bush

Twigs:
2. color of 1-year old twigs (a)
3. color of 1-year old twigs (b)

Thorns:
4. thorns always distinct from leafy short shoots
5. modal length
6. thickness at base
7. curvature
8. frequency
9. color on 1-year old twigs (a)
10. color on 1-year old twigs (b)

Leaves:
11a. size: length of blade (in mm)
b.*size: breadth at maximum point (in mm)
12a. shape: (char 11a/char 11b as %)
b. shape: distance from base to widest intersect on midvein
13. shape: location of widest point: (char 12b/char 11a as %)
14. shape: angle made by base of leaf to widest point (°)
15a. lobing: longest lobe, measured along vein (in mm)
b. lobing: deepest adjacent sinus (line ∥ base of sinus to tip of lobe, in mm)
16. leaf incision index, LII (char 15b/char 15a as %)
17. number of side veins
18. leaf base—angle to widest point of blade
19. extent of lobing: (no. of lobes where LII > 20%)
20. veins to obvious sinuses: (number of where LII > 20%)
21. lobing related to vein no.: (char 20/char 19 as %)
22. pubescence above
23. glandular teeth on serration tips or petioles
24. subevergreen to deciduous

Inflorescence:
25. bracteoles at anthesis
26. number of flowers
27. pedicel indumentum
28. pedicels punctate or not

Flowers:
29. hypanthium pubescence
30. calyx: shape
31. calyx: lobe-length
32. calyx: pubescence
33. calyx: serration/lobing
34. calyx: lobes, serrae (if any), gland-tipped
35. flower diameter, cupped (mm)

TABLE 4. (Continued).

36. gynoecium: style no.
37. androecium: anther no.
38. androecium: anther length
39. androecium: anther color when fresh; (no red, pink to purple)

Fruit:
40a. length, excluding calyx, fresh
b. diameter, fresh
41. diameter/length: (as %)
42. widest part: (in lower ⅓; middle ⅓; upper ⅓)
43. color when fresh and mature (yellow, red, black)
44. undamaged fruit highly pruinose
45. calyx tube (collar) present
46. calyx lobes present
47. nutlet no.
48. nutlet: strongly dorsally grooved
49. nutlet: laterally excavated

* 'b—subscripted' characters were measured, but later deleted as redundant because contributing to ratios.

as is advocated, for instance, in Phipps's "Bestblock" (1975b), but the biogeographical data type (distribution maps with smooth edges) does not conveniently permit the use of such sensitive methods. Nevertheless, if the scale of grid is neither too large nor too small, pattern is still well detected. From the presence-absence data, species' arrays may be compared by positive matching coefficient and clustering to generate distribution patterns, while additive scoring of individual grid squares directly generates counts of areas of high species richness.

A cautious approach to cladistics was used in view of the high likelihood of hybrid or alloploid situations (e.g., Phipps, 1984). Phenetic screening of the 25 or so maloidean genera (Table 9) was conducted to identify a set of genera most closely related to *Crataegus* from which a sister-group could be generated. This set of genera constitutes the tribe *Crataegeae* Koehne. Outgroup analysis of Crataegean genera contributed to the identification of ancestral character states. Some 18 characters (subset of 49 used for the phenetic analysis) were thereby selected as confidently polarisable. A simple transform program recoded the characters with polarity. Details of the specific transforms may be found in the discussion of the cladistic results. Although available, most well-known cladistic programs that operate on a polarized character matrix were not used because

TABLE 5. Character selection and polarity for cladistic analysis.

Character No.	
1.	*OTU identifier*
	Coded descriptors
	0 = prim.; +ve and −ve numbers indicate advancement in various directions
	Habit
2.	tree (prim.) → small shrub (adv.)
	Branches
3.	thornless with sharp-tipped short shoots (prim.) → short thorns → long thorns (adv.)
	Leaves
4.	subevergreen (prim.) → early deciduous (adv.)
5.	multiveined (prim.) → few veined (adv.)
6.	angle of side-vein with midrib narrow (prim.) to wide (adv.)
7.	leaves unlobed (prim.) → deeply lobed (adv.)
8.	veins to leaf sinuses lacking (prim.) → present (adv.)
	Inflorescence and flowers
9.	pedicel indumentum dense (prim.) → glabrous (adv.)
10.	hypanthium indumentum dense (prim.) → glabrous (adv.)
11.	flowers medium in size (prim.) ↗ very large (adv.) ↘ small (adv.)
12.	calyx lobes entire (prim.) → serrate (adv.)
13.	carpel number medium (prim.) ↗ low (adv.) ↘ high (adv,)
14.	anthers white or cream (prim.) → purple (adv.)
15.	anther number 20 (prim.) → 10 → 5 (adv.)
	Fruit
16.	fruit oblate (prim.) → spherical → long (adv.)
17.	fruit large (prim.) → small (adv.)
18.	fruit yellowish (prim.) → reddish → black (adv.)
19.	nutlet dorsally smooth (prim.) → ridged (adv.)

they always generate furcations, not necessarily desirable in a group such as *Crataegus*. Instead, program PRIMO, which successively finds hypothetical taxonomic units (HTUs) (nodes) uniting most similar pairs of OTUs and HTUs, was run until patristic distances became too long according to a test criterion and were held likely to generate ambiguous or wrong results. The program also incorporates the capability of indicating putative hybrid situations where two or more alternative fusions show similar patristic distances within specified upper bounds. The result shown here is thus a pro-cladogram displayed in target diagram style, which postulates certain likely connections and proves to recapitulate the tighter phenetic groupings.

Conformable phenetic, biogeographical, and pro-cladogram patterns are held to be strongly evidentiary of true cladistic relationships.

EXTRINSIC DATA

Long-distance dispersal potential, and thus mode of propagule dispersal, paleogeography and paleoclimate are critical to a full evolutionary understanding of a genus. These phenomena are considered in the discussion section, to the extent for which they are understood to date.

PHENETIC RESULTS

Using all 49 morphometric characters or only 14 leaf characters, very similar groupings of *Crataegus* emerge (Figs. 5–8). Coded on these diagrams are leaf glyphs (Figs. 5–8) and thorn glyphs

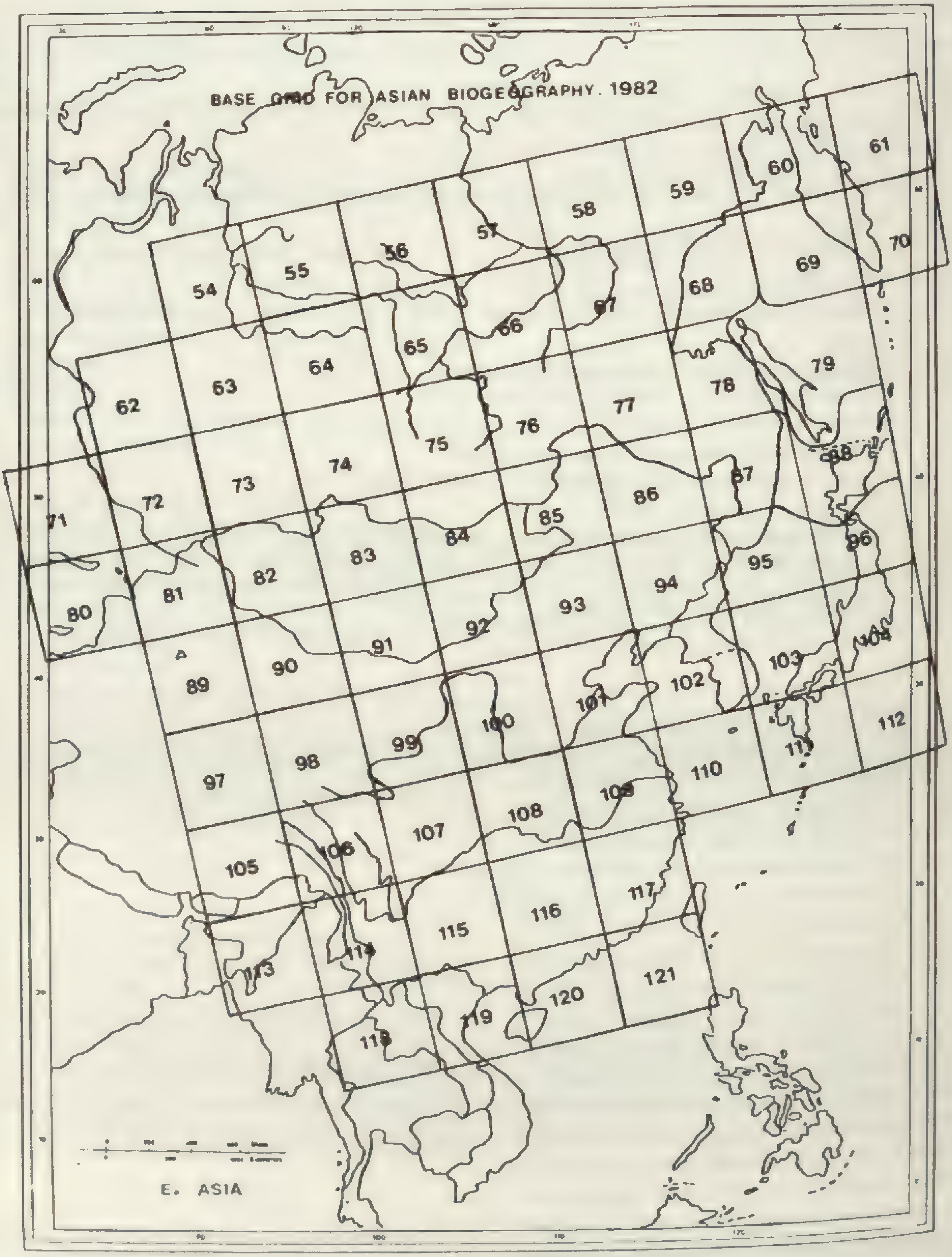


FIGURE 3. Equiform grid for eastern Asia.

(Figs. 5, 6), of which also fit well. The main groupings found are as follows:

a) Leaves narrow, multiveined, essentially unlobed:
   i) with thorny short shoots: *C. mexicana, C. scabrifolia*
   ii) with true thorns: ser. *Crus-galli, Punctatae*

b) Leaves usually small, broad, deeply lobed. veins to leaf sinuses:
   i) with thorny short shoots: *Azaroli, Oxyacanthae*
   ii) with true thorns e.g. *C. marshallii* (US), *C. pinnatifida* (China)

c) Trees of forest shade; fruit smallish; true thorns present; distribution SE United States

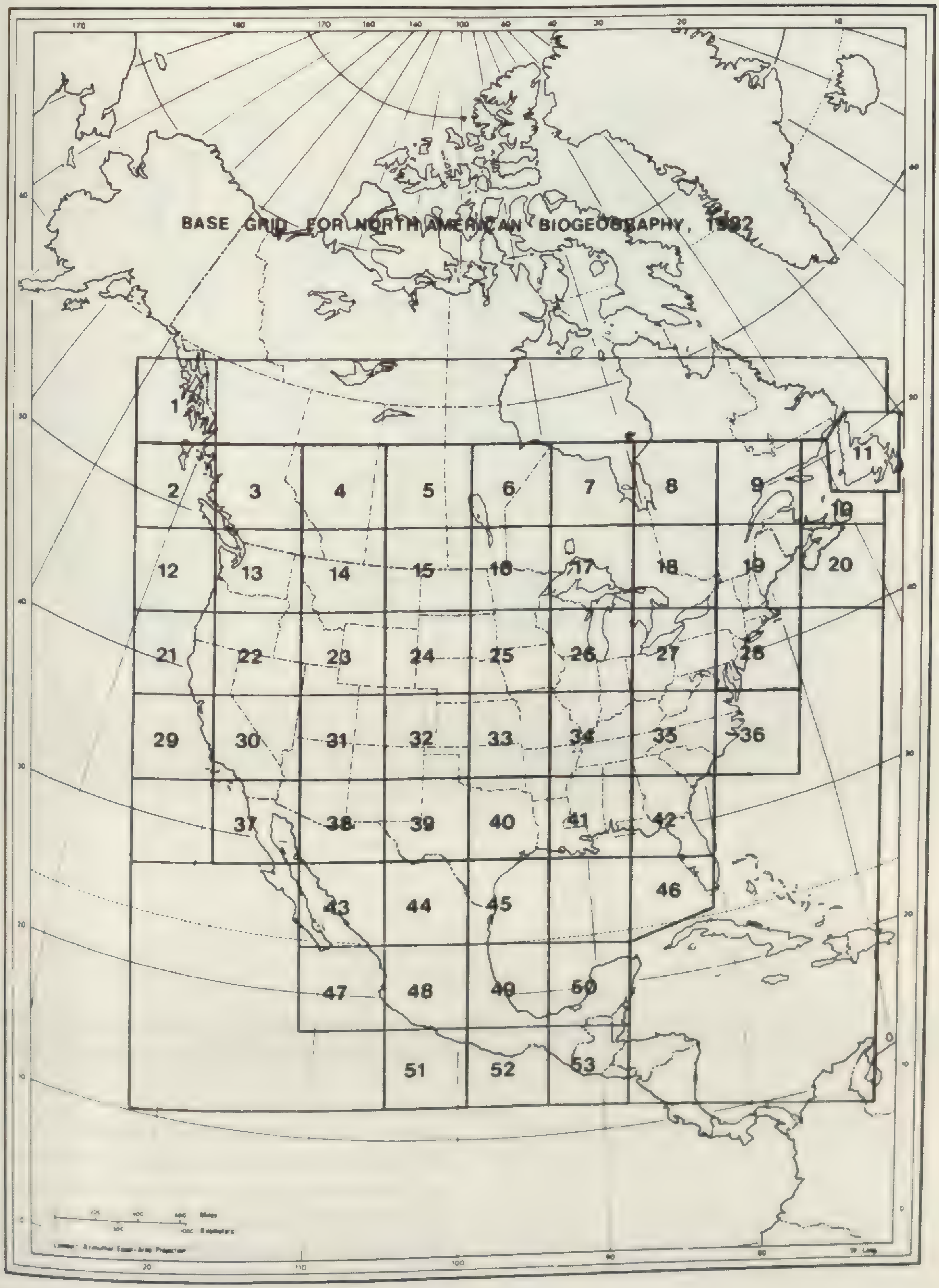


FIGURE 4. Equiform grid for North America.

i) Leaves trilobed: sect. *Cordatae* (*C. phaenopyrum* only)

ii) Leaves otherwise (ser. *Virdes, Parvifoliae, Brevispinae,* etc.)

d) Leaves shallowly lobed, broader, ovate, obovate, broad-elliptic to ± deltoid; true thorns present:

i) most N. American taxa. This group corresponds to El-Gazaar's '*Americanae*' and it will probably be well justified to erect a

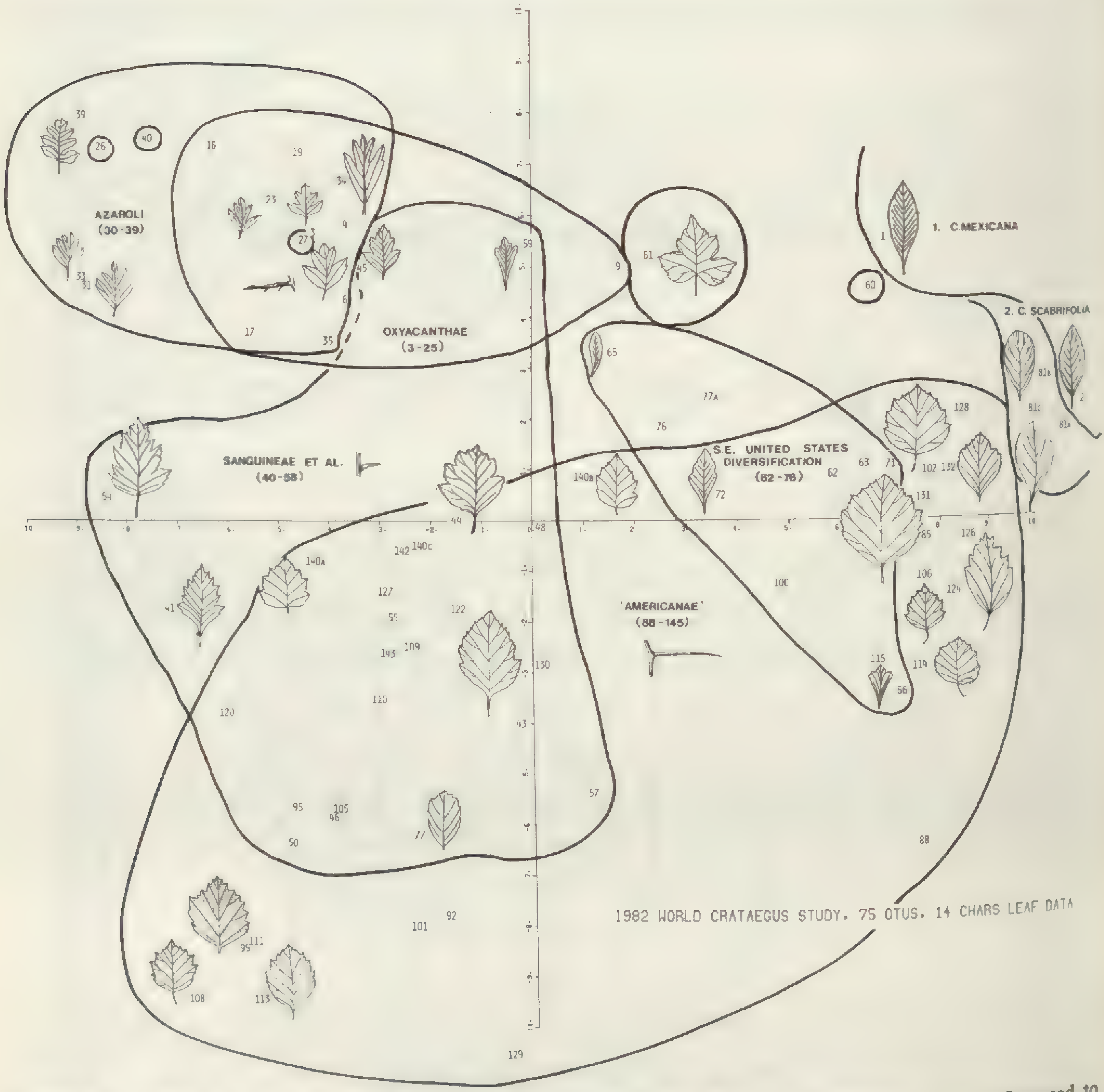


FIGURE 5. Plot of q-PCA, first two axes, 75 individuals, leaf data. (OTU numbers cross-referenced to Appendix A.)

section of this name. However, I feel that this is premature while the boundaries remain uncertain.

ii) Some East Asian taxa (e.g. *C. kansuensis, C. maximowiczii*). These have shorter thorns than most '*Americanae*.'

e) Some miscellaneous leaf shapes, e.g. *C. spathulata* (US), *C. flava* (US), *C. cuneata* (China)

In the components analyses (Figs. 5 and 6) *Azaroli* and *Oxyacanthae* strongly overlap and are opposed on the first two factors by the '*Americanae*' and *Crus-galli* types. Notably, *C. mexicana* and *C. scabrifolia* are closer to *Azaroli-Oxyacanthae* when all characters are considered than when leaves only are treated, when they are polar to the aforementioned groups. The Sino-Siberian taxa (sect. *Sanguineae*, et al.) overlap the *Azaroli-Oxyacanthae* using all data but overlap only '*Americanae*' on leaf data. This reflects an essentially intermediate position for the *Sanguineae*. Likewise, the southeastern United States diversification is fully overlapped by the '*Americanae*' for leaves only, but has a central tendency and barely overlaps when using all data. Finally when leaves only are considered, the '*Americanae*' are not only variable but almost fully overlap both the Sino-Siberian groups and the southeastern United States groups. Thus, on all counts, the *Americanae* and *Oxyacanthae-Azaroli* are the most contrasted pair, while all the other taxa are in some ways intermediate between *Americanae*

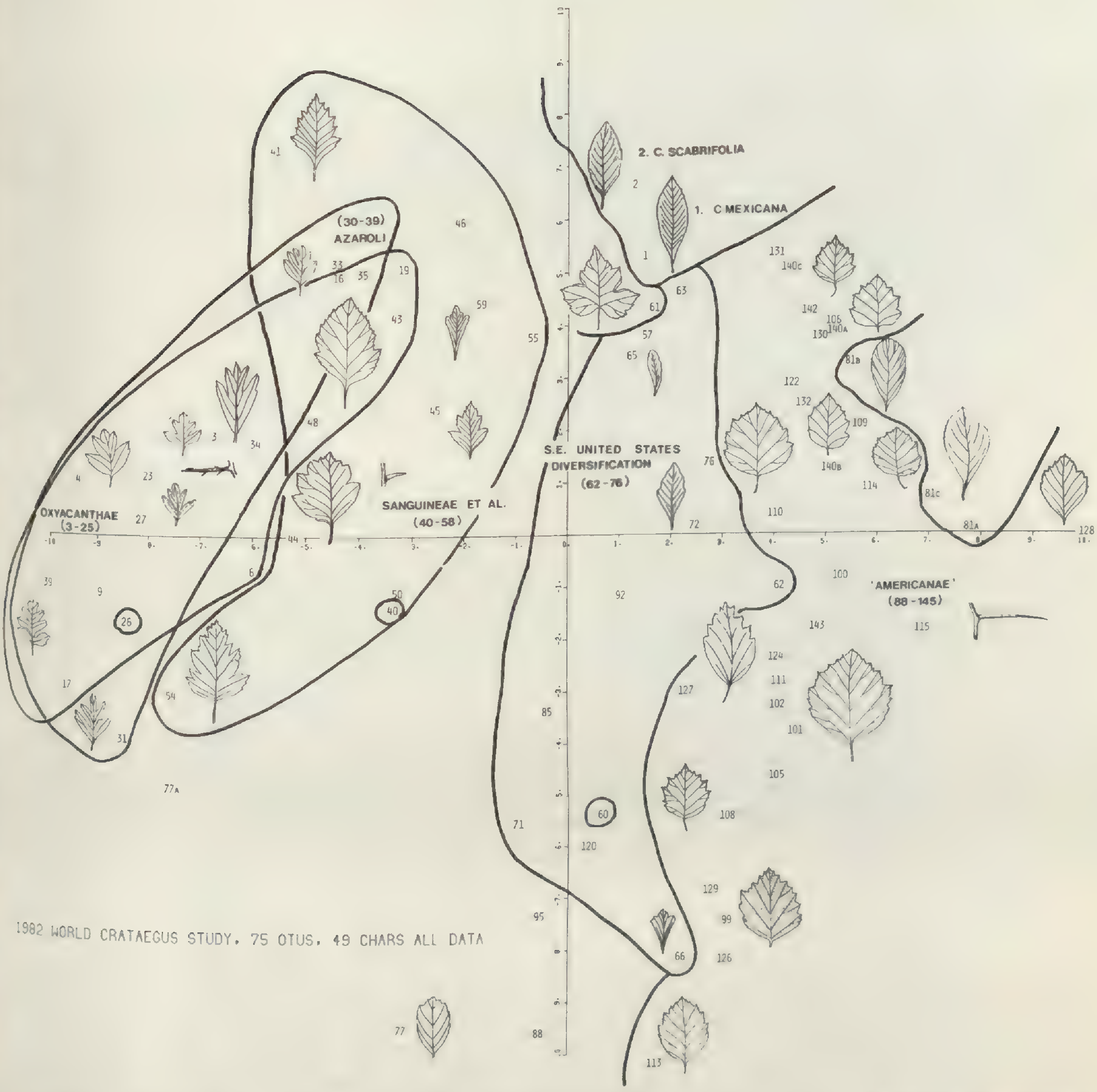


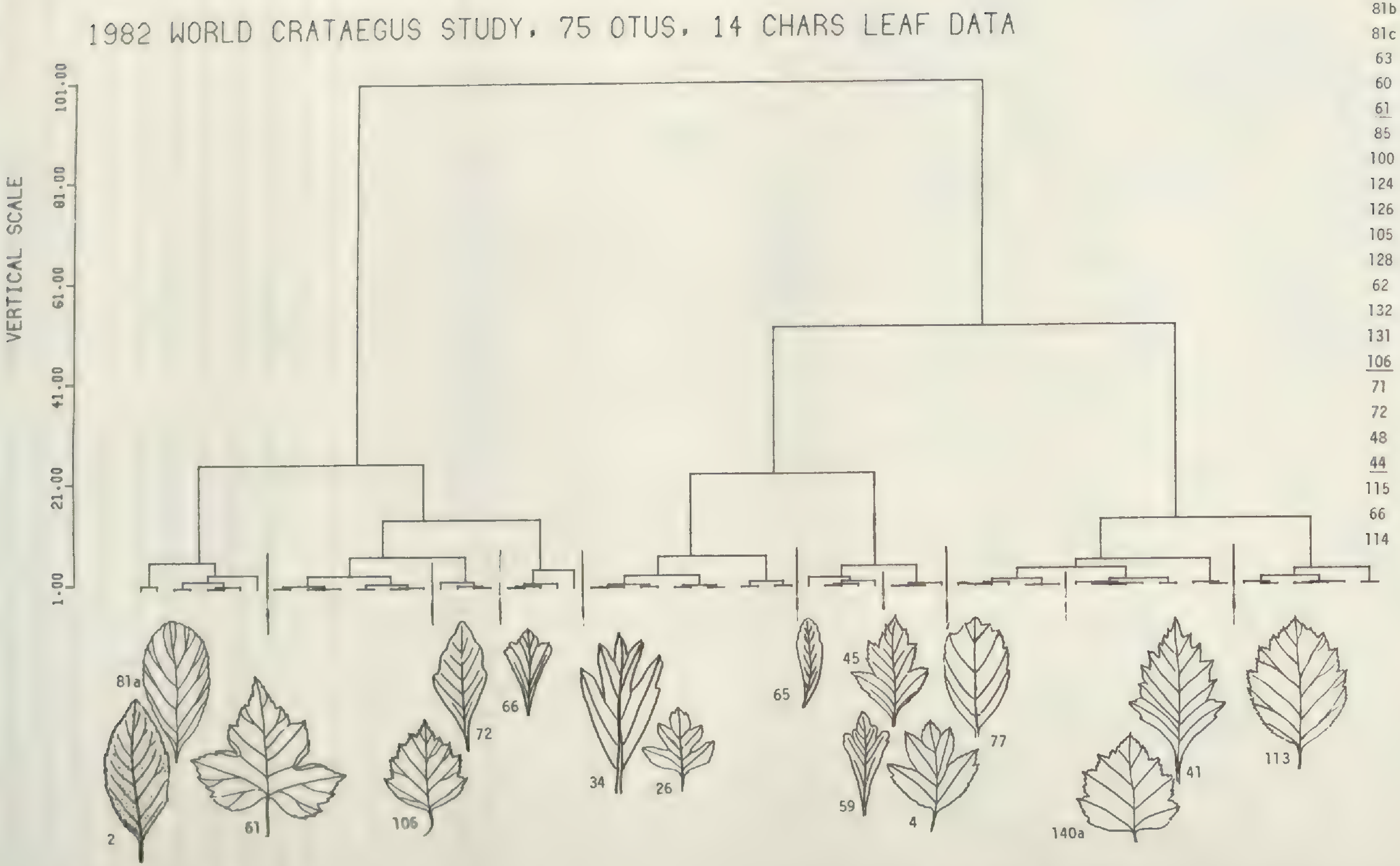
FIGURE 6. Plot of q-PCA, first two axes, 75 individuals, all data. (OTU numbers cross-referenced to Appendix A.)

and *Oxyacanthae-Azaroli.* This, of course, has a striking cladistic significance.

The dendrograms (Figs. 7 and 8) lend detail to the two-dimensionality of the scattergrams. Notable additional information involves the relative isolation of *C. hupehensis* and *cuneata* as well as American sect. *Flavae.* Also, the dendrogram for all data (Fig. 8) shows an interesting differentiation between more glabrous and more pubescent groups, especially in the '*Americanae.*' The biological significance of this is not understood, but when it is it should aid cladistic analysis.

R-type components analyses indicate (Table 6) the very strong significance of leaf-lobing and related characters though the loading (72%) of character 10 (pubescence) on root 3 may eventually appear to be highly significant. When considering all characters (Table 7) the major ones almost equally divide between inflorescence pubescence and related characters on the one hand and high ranking leaf characters on the other. There is clearly some broad correlation between leaf morphology and other variables indicated here which accounts for similarities in the q-PCAs and which relate to the observation in the previous paragraph.

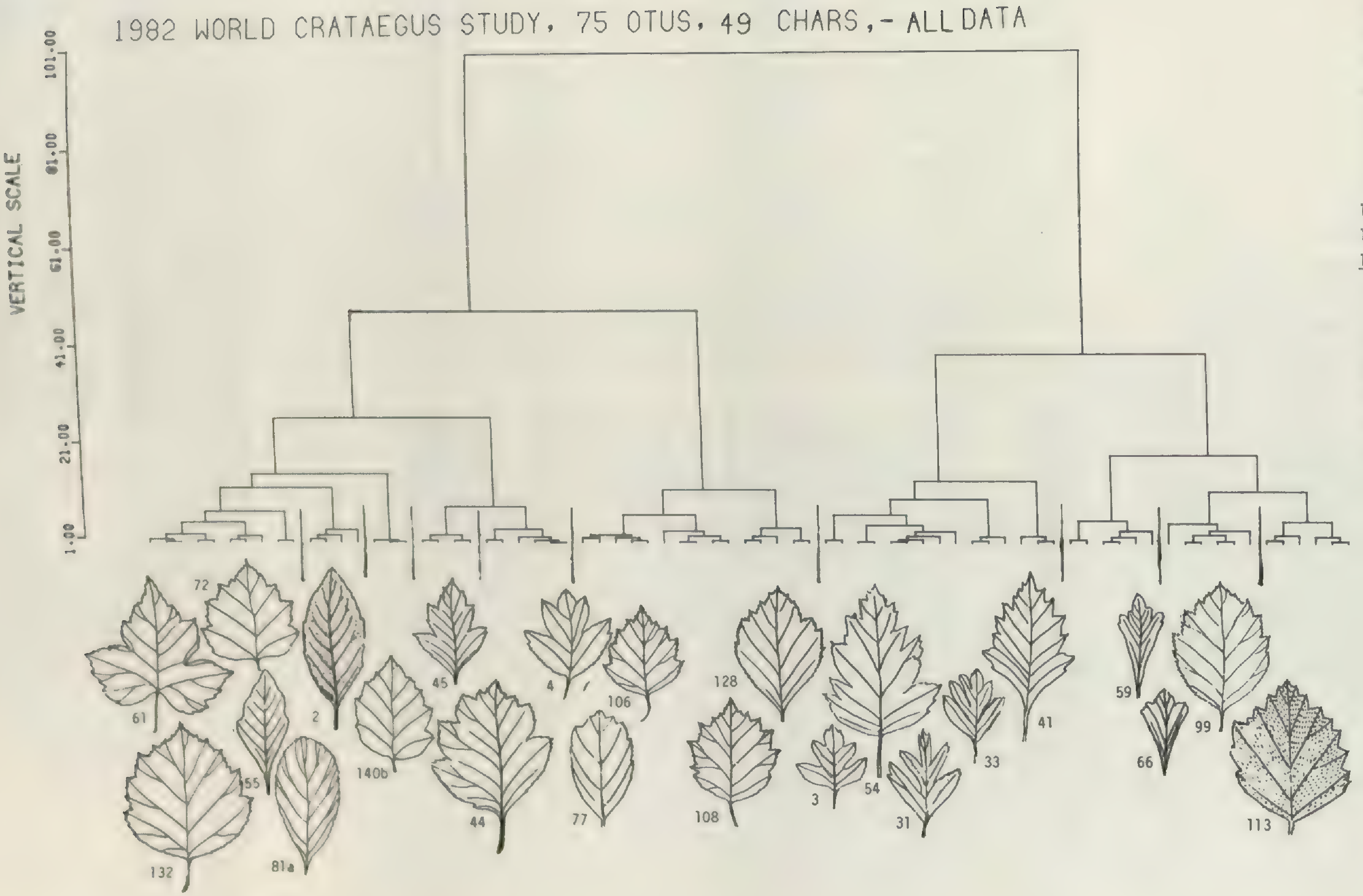
Thus, although the presence of some intermediate taxa, together with the existence of a broad amplitude for some species groups, do not



OTU NUMBER, left to right

2	88	77
1	57	130
81a	3	43
81b	23	109
81c	34	110
63	35	143
60	27	127
61	26	122
85	39	142
100	31	140c
124	33	140a
126	40	55
105	16	41
128	54	120
62	17	50
132	65	46
131	140b	129
106	76	101
71	9	92
72	59	113
48	45	111
44	6	108
115	4	99
66	19	105
114	77a	95

FIGURE 7. Phenogram derived from minimum variance clustering of 75 individuals, leaf data. (OTU numbers cross-referenced to Appendix A.)



OTU NUMBER, left to right

61	6	33
132	4	43
62	77a	48
63	77	41
60	106	65
131	130	34
72	142	35
55	127	85
81a	122	71
81b	110	102
1	109	126
2	108	59
76	81c	66
57	124	129
140a	128	101
140b	115	92
140c	114	99
50	3	95
46	26	88
45	54	113
44	17	111
40	39	120
19	31	143
16	23	100
9	27	105

FIGURE 8. Phenogram derived from minimum variance clustering of 75 individuals, all data. (OTU numbers cross-referenced to Appendix A.)

TABLE 6. 1982 *Crataegus* study, r-type components analysis, leaf data.

Percent of Trace a/c by Each Root		Characters Contributing more than 10% Each to First Three Roots		
		Root 1	Root 2	Root 3
Root 1	32%	no. 7, 41% no. of deep lobes per leaf	no. 11, 36% glandular serrations on leaf & petiole margin	no. 10, 72% pubescence above
Root 2	22%	no. 9, 32% percent veins ending in lobes	no. 8, 31% veins to sinuses of leaves	
Root 3	13%	no. 8, 11% veins to sinuses per leaf	no. 5, 11% leaf incision index	
Root 4	10%			
Roots 5–14	23%			
	100%			

Character 5, leaf incision index contributes most, 10.3% on all roots combined.

generate an utterly sharp taxonomy, there can be no doubt that the taxonomic groups recognized are broadly valid.

BIOGEOGRAPHIC RESULTS

The phenogram (Fig. 9) derived from the gridded distributional data shows that species ranges fall strongly into readily identifiable groups. Bearing in mind that there is a slight overlap between the *Sanguineae* (e.g. *C. sanguinea* Pall. ex Bieb.) and some species of the *Oxyacanthae* and *Azaroli* in the Soviet Republics of Kazhak, Kirghiz and Tadzhik, the European and west Asian taxa are mainly very strongly cut off from those under discussion here. The first division of our phenogram necessarily differentiates Asiatic from North American taxa because there are no species common to the two areas.

Characteristic Asiatic distributions are represented in Figures 10–12. Basically a northern (N of 40°N lat.) group of species and a southern group may be recognized. In the northern group, the wide-ranging *C. sanguinea* (Fig. 11) achieves the most northerly distribution of extant *Crataegus* (63°N lat.). *Crataegus maximowiczii* (Fig. 10) and *C. pinnatifida* (Fig. 12) of NE Asia and *C. chlorosarca* (Fig. 10) of the Pacific Rim (N to Kamchatka) are of interest in their approach to Beringia. Presumably a quite small climatic shift could permit *C. chlorosarca* to migrate to the New World. More southerly species are represented by *C. kansuensis* (Fig. 11) of north-central China and the taxonomically isolated *C. cuneata* (Fig. 10) widespread in warm temperate and southeast China. Several species of restricted distribution in western China proper are known, of which the taxonomically isolated *C. scabrifolia* (Fig. 12) of Yunnan is a particularly good example. The wide-ranging *C. aurantia*, with a northerly distribution, is not illustrated. There is a clear demarcation between northerly 'sanguineoid' forms and southern and central taxa that are largely unrelated to each other or anything

TABLE 7. 1982 *Crataegus* study, r-type components analysis, all 49 characters.

Percent Trace a/c by Each Root		Major Characters Contributing to First Three Roots		
		Root 1	Root 2	Root 3
Root 1	18%	no. 23, 30% hypanthium pubescence	no. 6, 20% gland-tipping of calyx lobes	no. 15, 17% number of deep lobes
Root 2	15%	no. 22, 24% pedicel indumentum	no. 25, 16% lobing of calyces	no. 17, 14% lobing/vein number
Root 3	10%	no. 18, 8% pubescence upper side of leaves	no. 16, 10% veins to obvious sinuses	no. 4, 12% color on 1-year old twigs
Roots 4–49	58%			
	100%			

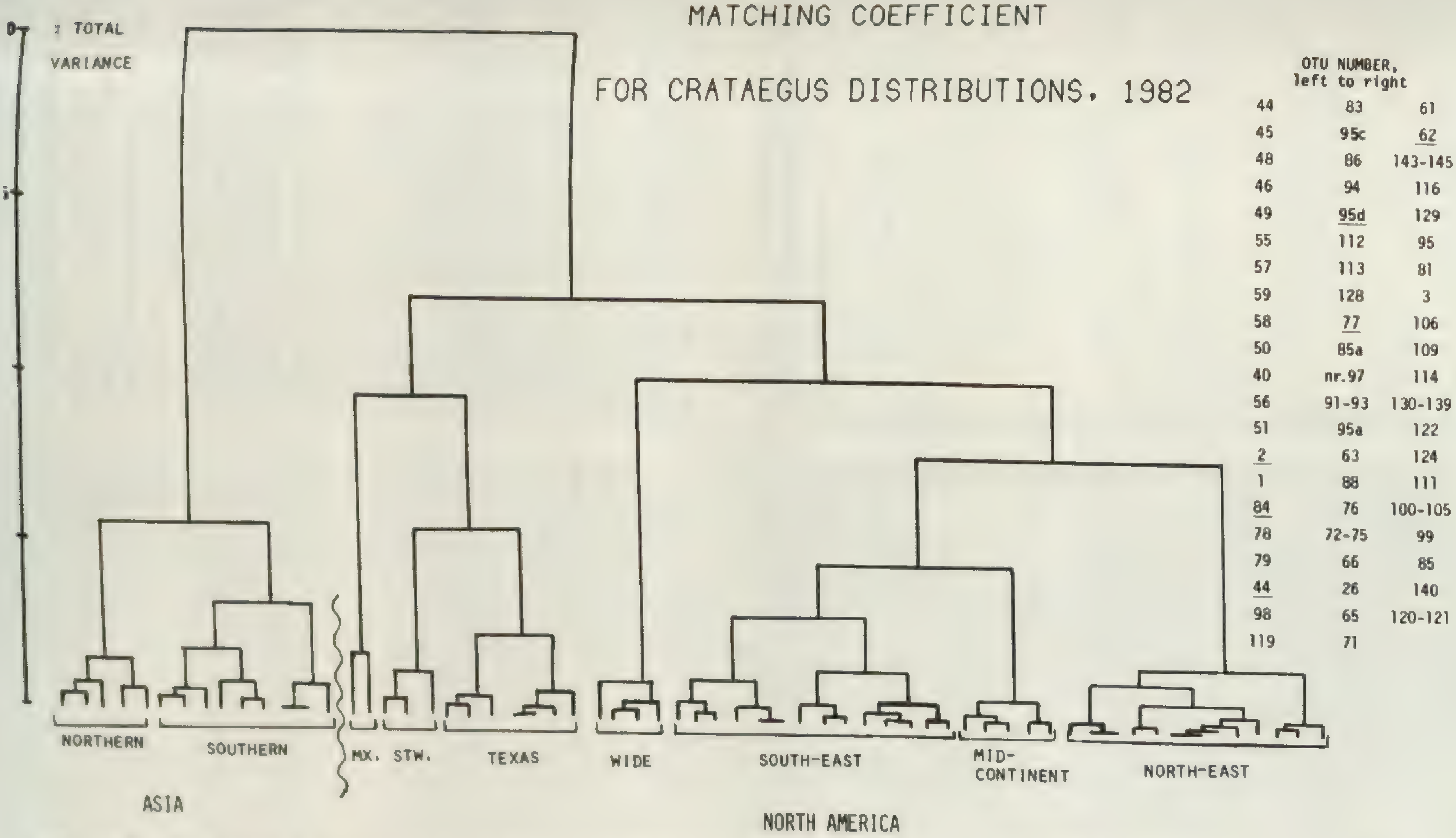


FIGURE 9. Classification of distributions derived by minimum variance clustering of positive matching coefficient. (OTU numbers cross-referenced to Appendix A.)

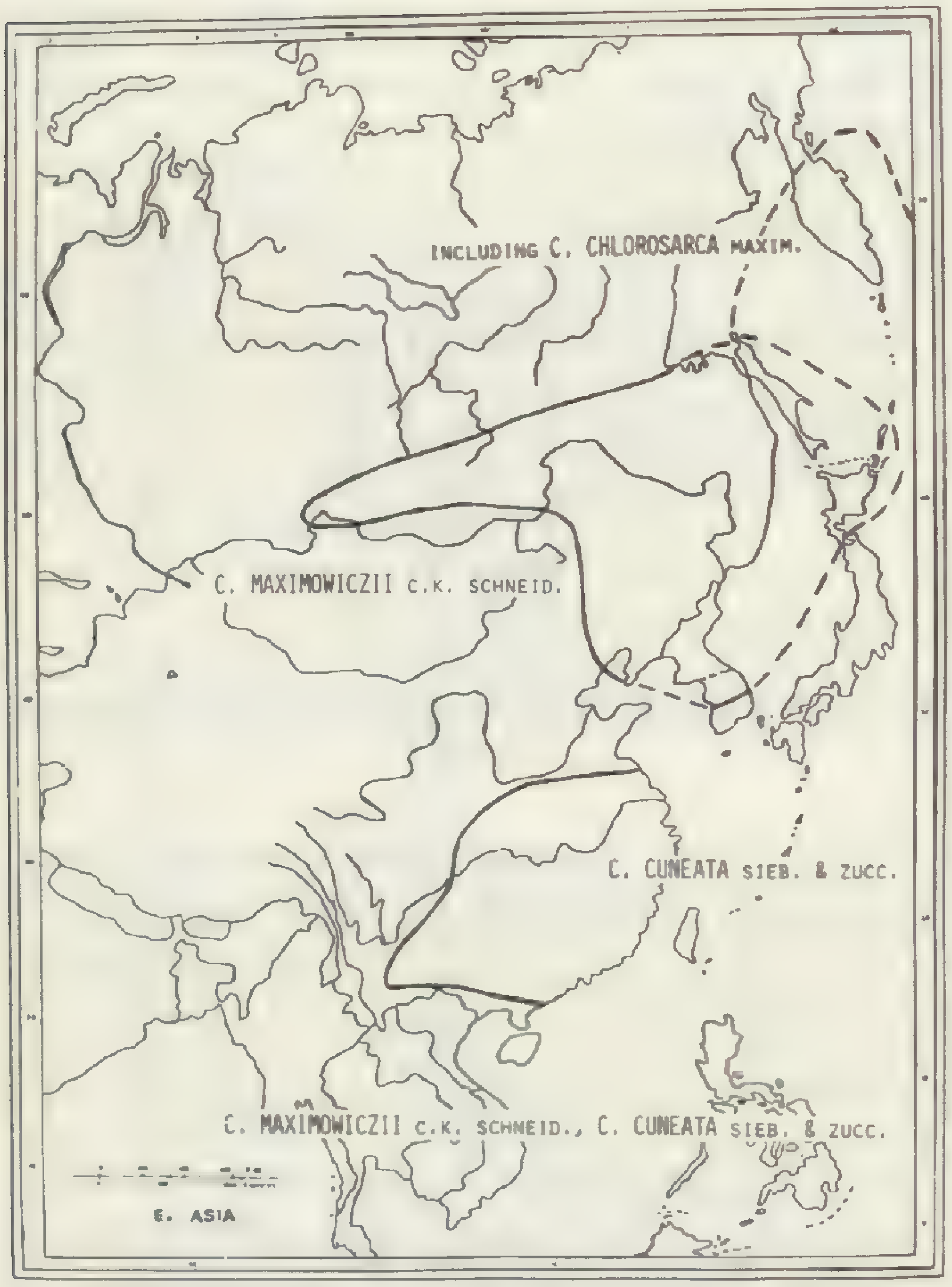


FIGURE 10. Distribution of *Crataegus*: *C. maximowiczii* C. K. Schneid., *C. cuneata* Sieb. & Zucc.

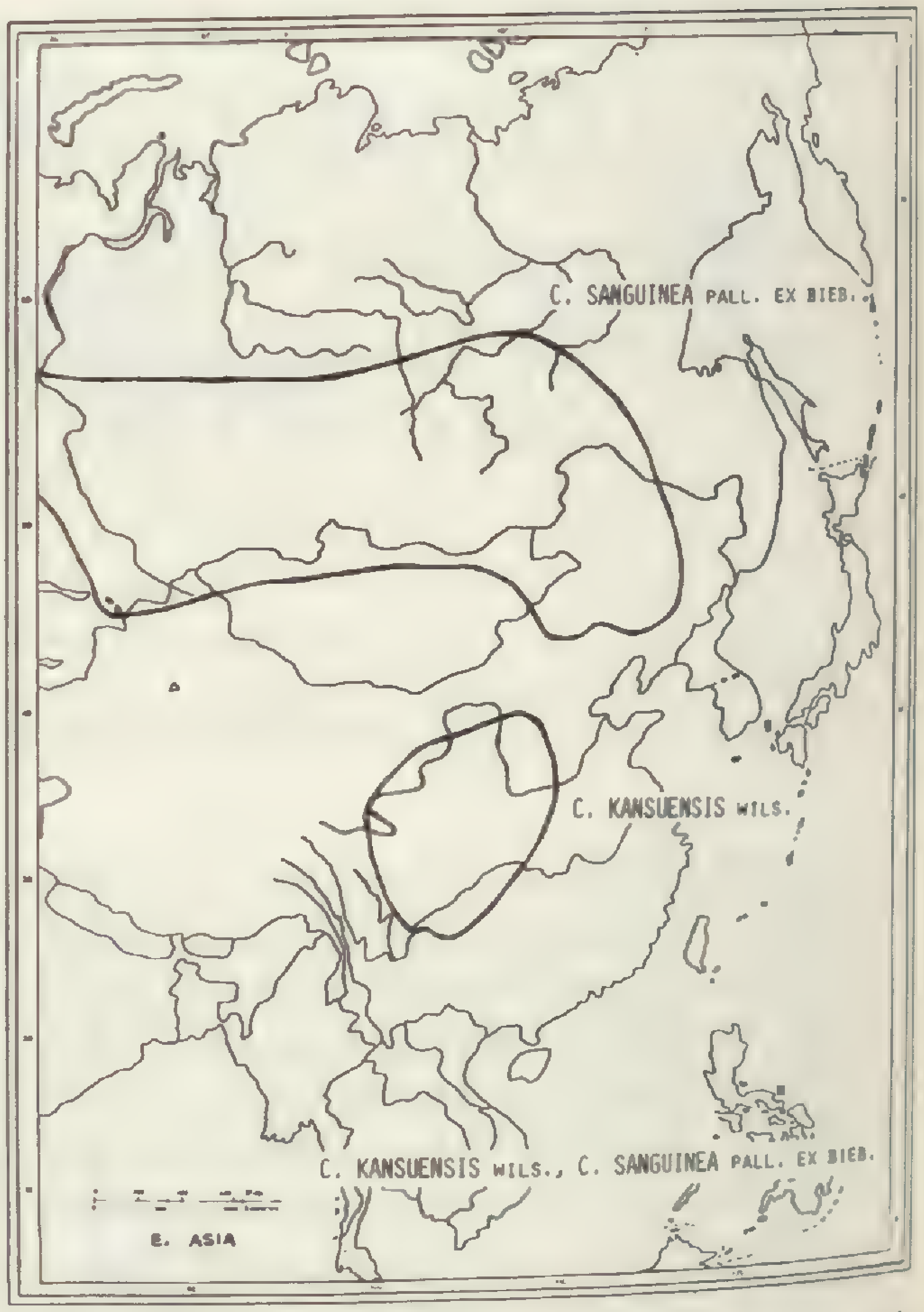


FIGURE 11. Distribution of *Crataegus*: *C. sanguinea* Pall. ex Bieb., *C. kansuensis* Wils.

else (e.g. *C. hupehensis*—not shown, *C. scabrifolia* and *C. cuneata*).

In North America, western, Mexican, Texan, southeastern, eastern, northeastern and wide ranging types stand out. There are few western species but *C. douglasii* (Fig. 13), mapped to include the possibly conspecific *C. rivularis*, is notable for its extreme northerly range extension in the Anchorage region of Alaska, remarkably near to Beringia. It should be noted that *C. douglasii* is one of the few North American species to share the short stout thorns characteristic of the sanguineoid group from Asia. *Crataegus douglasii* exhibits the migratory potential of the genus with its disjunct population around the northern Great Lakes. *Crataegus columbiana* (not mapped) would link *C. chrysocarpa* (Fig. 17) to the Pacific, if conspecific, which it is close to being. The Mexican group is dominated by the quite wide ranging *C. mexicana*, which extends through the highlands into Guatemala. It is found under similar latitudinal and climatic conditions to its closest relative, *C. scabrifolia*, of Yunnan. Texas manifests a rich variety of *Crataegus*, several of which, of quite unrelated series (e.g. *C. viburnifolia–Molles*, *C. tracyi–Crus-galli*) are endemic there. Another important biogeographic group are the Gulf Coast and southeastern United States species. What is notable about these is their lack of relationship to each other or, with the odd exception, to species outside this region. In this they parallel the mutually unrelated southern Chinese taxa (see above) and reinforce the notion that they resulted from old radiations in these regions. The pertinent United States taxa are ser. *Aestivales* (Fig. 14), ser. *Flavae* (unmapped), *C. marshallii* (Fig. 17), most closely related to European *Oxyacanthae*, *C. brachyacantha* of the Gulf Coast (not mapped), and the species of distinct series *Virides*, *Pulcherrimae*, *Cordatae*, and *Parvifoliae*. It is notable that all these are well differentiated from the northeastern United States taxa—mainly '*Americanae*'—and that most are somewhat shade-tolerant small trees. Mid-continent taxa are represented by *C. mollis* (Fig. 13). The northeastern taxa are dominated by '*Americanae*' species in high abundance, e.g. *C. macrosperma* (Fig. 19), *C. margaretta* (Fig. 16), other members of their series, and most of the *Silvicolae*, *Dilatatae*, *Pruinosae*, *Macracanthae*, and *Coccineae*. It is interesting to note that taxa with a large north-south range

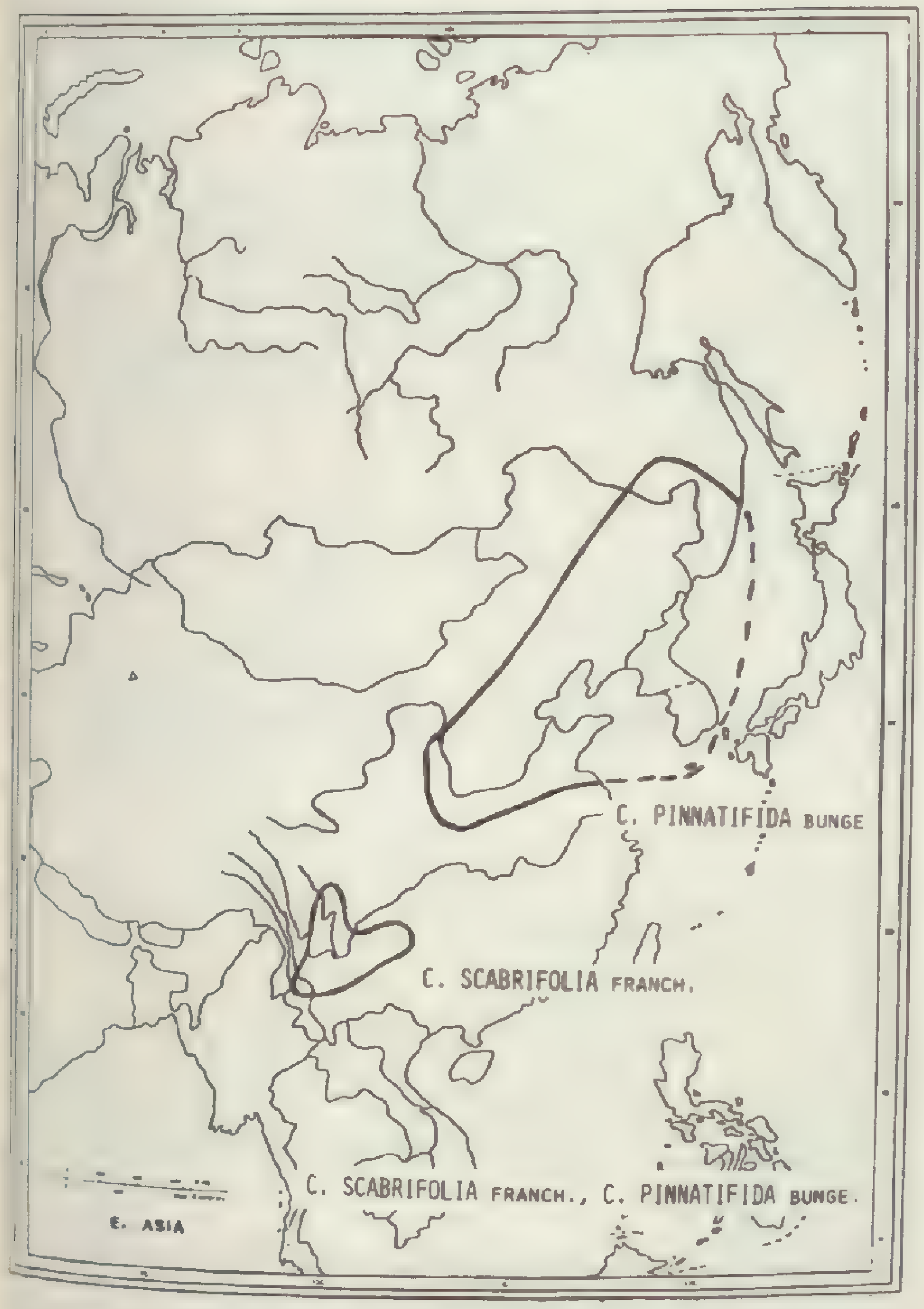


FIGURE 12. Distribution of *Crataegus*: *C. scabrifolia* Franch., *C. pinnatifida* Bunge.

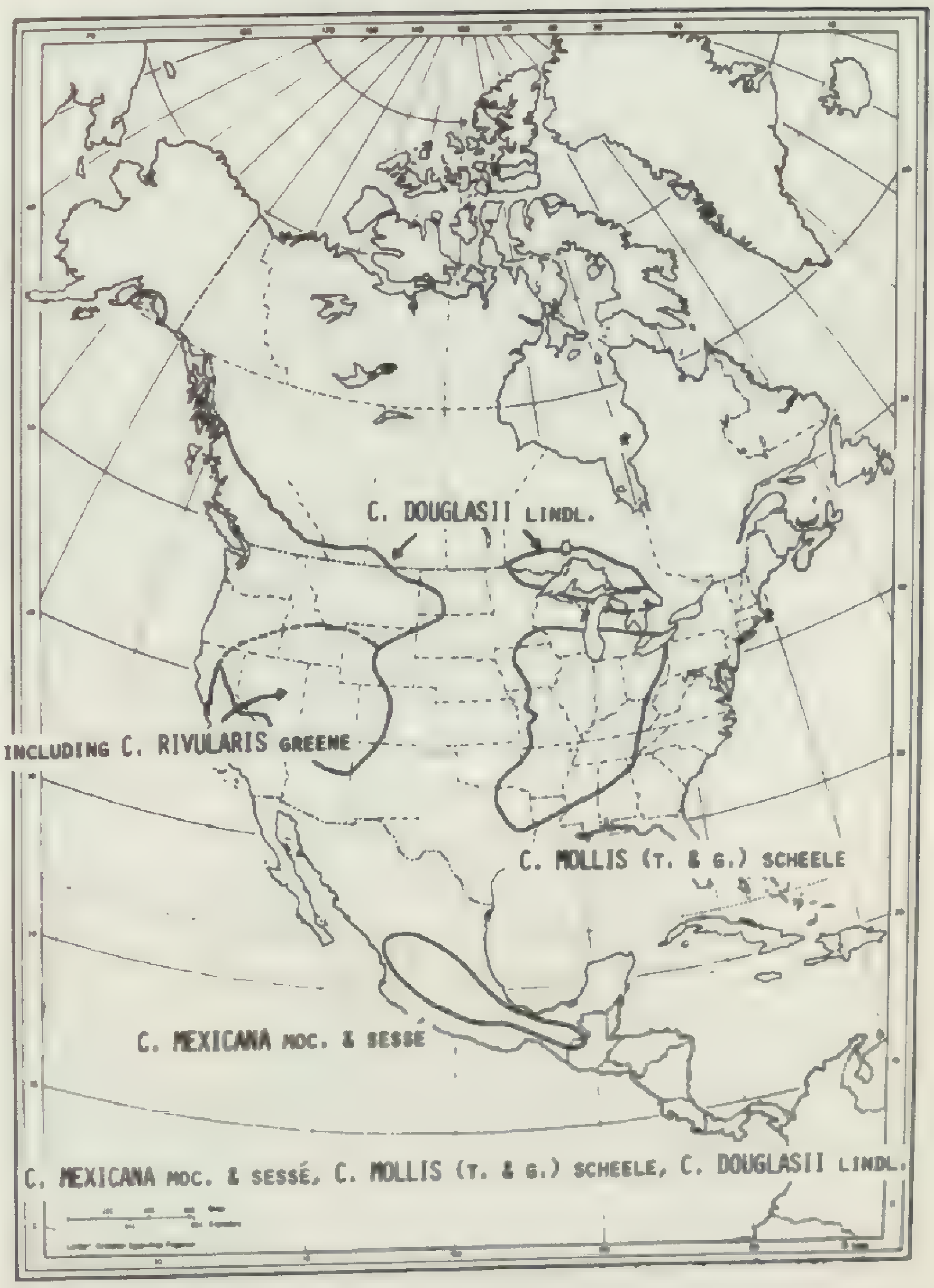


FIGURE 13. Distribution of *Crataegus*: *C. mexicana* Moc. & Sessé, *C. douglasii* Lindl., *C. mollis* (T. & G.) Scheele.

in the east, e.g. *C. crus-galli* sens. lat. (Fig. 15) and ser. *Punctatae* (*C. punctata* + *C. collina*) (Fig. 18) are neither 'Americanoid,' nor of southeastern United States relationship. Finally, some smaller series concentrated in the middle latitudes in the eastern United States must be recorded. *Bracteatae, Triflorae, Intricatae* should be noted. One of these, *C. harbisonii* (Fig. 19) is mapped and there are indications that all of these groups may represent descendants from fairly recent '*Americanae*'–*Flavae* introgression. Several of the northeastern taxa range southward down the spine of the Appalachians. Even more than in Asia, taxonomic groups match biogeographical patterns.

In summary, if we consider the three major continental areas: Europe and western Asia, eastern Asia, and North America pairwise, the taxonomic relationships are as follows:

a) Europe, western Asia/eastern Asia
—little similarity except slight overlap at interface
b) Europe, western Asia/North America
—no similarity, except *C. marshallii*
c) eastern Asia/North America
—several similarities: *Sanguineae, Americanae, C. scabrifolia, C. mexicana*

With regard to areas of species' richness, eastern North America as a whole stands out as far richer than eastern Asia, western North America or Mexico (Figs. 20, 21). This cannot be accounted for merely on the basis of differing taxonomic resolution of species' limits, especially because a conservative approach has frequently been made for North America by substituting single series for whole sets of species. The extreme richness of Appalachia, however, is partly an artefact of the size of grid square chosen since lowland (southeastern) species may commingle in a single grid square with predominantly northern (here mid-Appalachian) species.

The biogeographic results are rich interpretively. One notes (Fig. 21) the predominance of species in the deciduous forest biome of the Eastern United States and Europe-Russia (latter not mapped). Northward the genus may be largely delineated by the January mean −10°F isotherm, +10°F in North America (Fig. 22a, b) or, perhaps more adequately, by the southern edge of the coniferous forests. Southeastward, in two con-

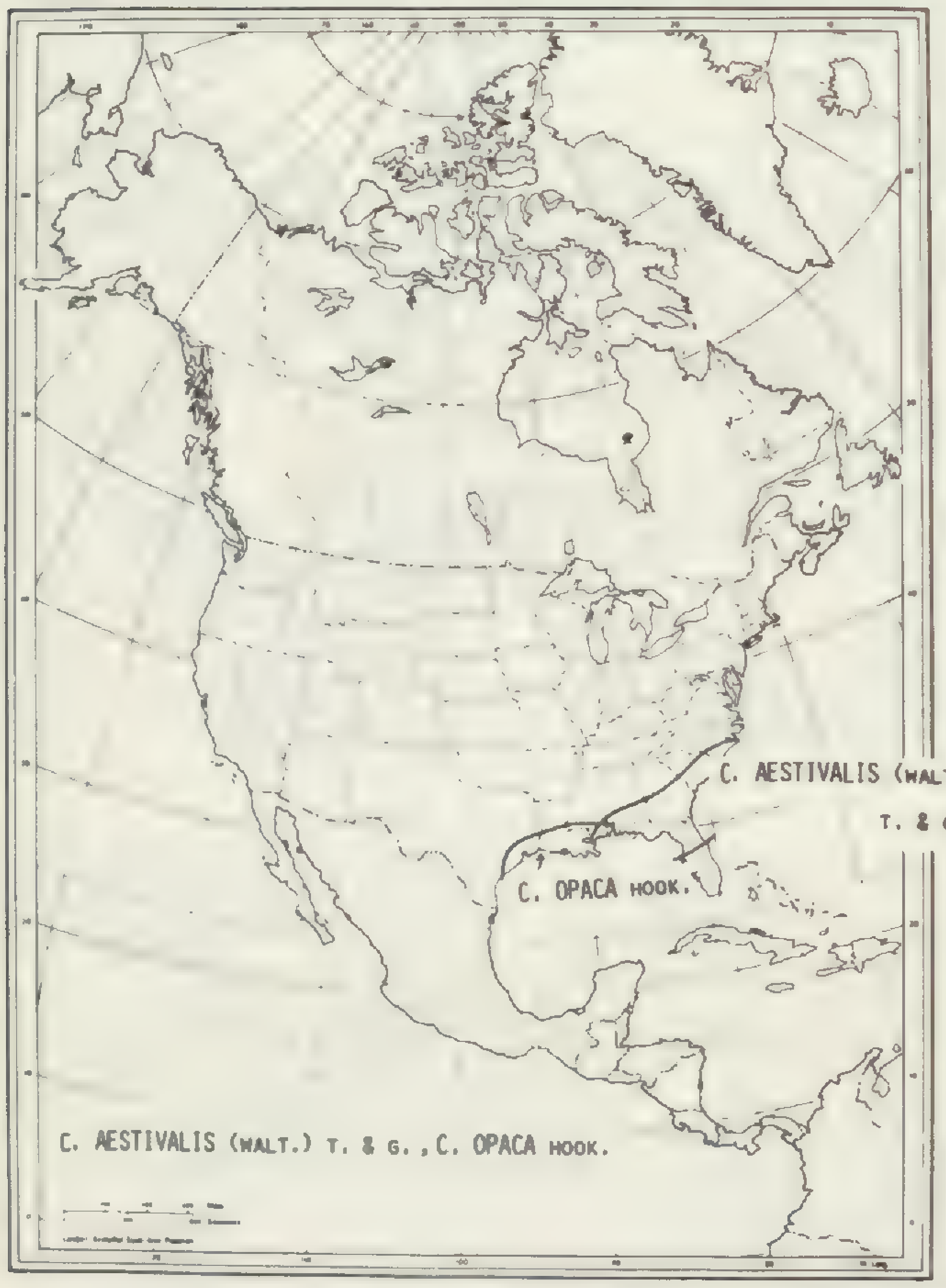


FIGURE 14. Distribution of *Crataegus*: *C. opaca* Hook., *C. aestivalis* (Walt.) T. & G. Note—encoded as *C.* sect. *Aestivales.*

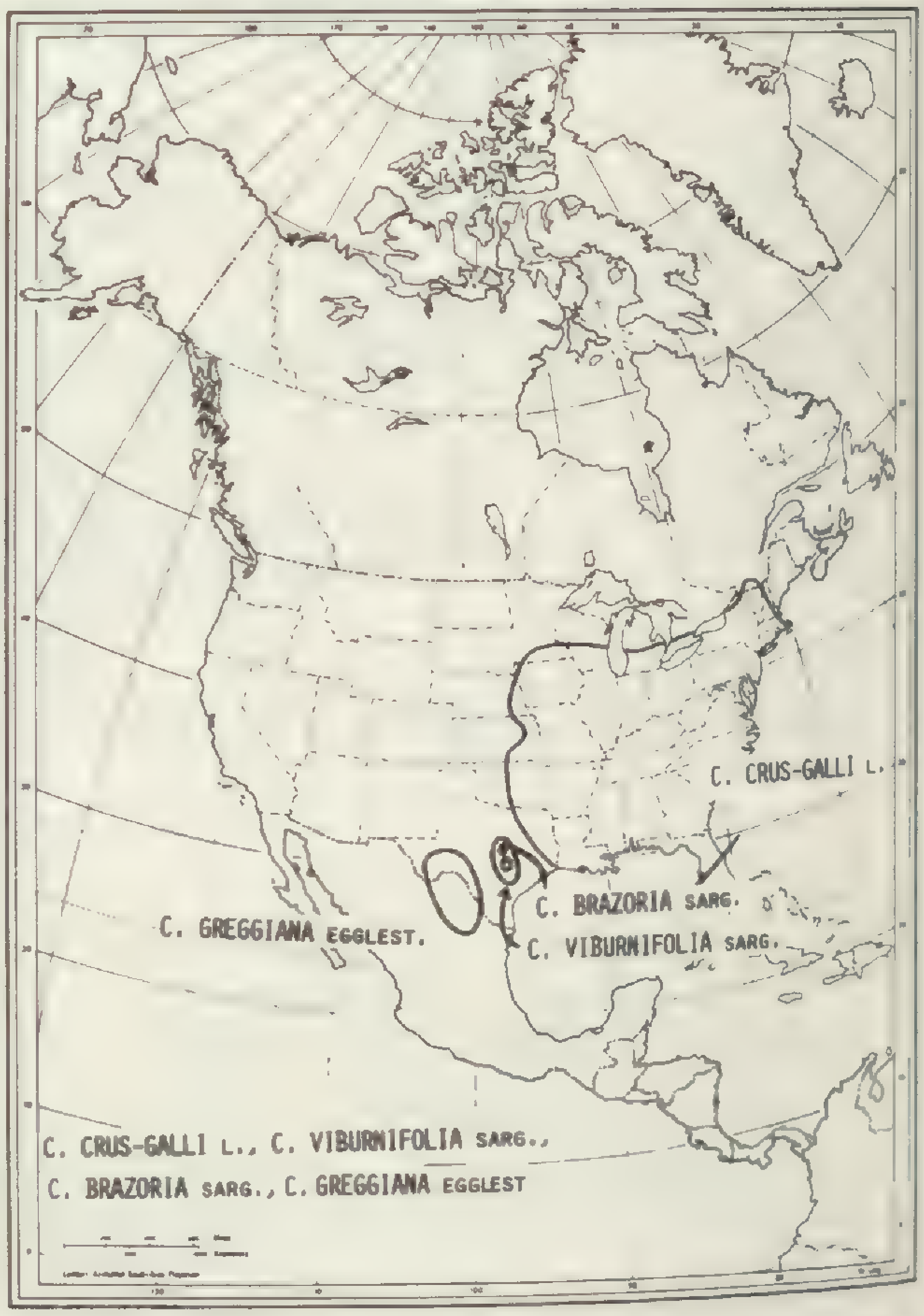


FIGURE 15. Distribution of *Crataegus*: *C. greggiana* Egglest., *C. viburnifolia* Sarg., *C. brazoria* Sarg., *C. crus-galli* L.

tinents, warm climates (? mild winters) and subevergreen conditions appear limiting. Only one species, *C. cuneata,* occurs in southeast China (Fig. 10), and that not in Hainan, while central Florida represents the southeastern range limit for the United States. Although one is tempted to relate the southeastern continental limits of *Crataegus* to climax habitat type (trend to evergreen forest), in view of the success of other maloids in such areas (e.g. *Photinia*) this may obscure a more direct physiological relationship, perhaps that of a lack of adequate winter chilling requirements southward.

In the southeast and southern coastal plains of the United States, two ecological-adaptive groups stand out. One is the somewhat shade-tolerant tree-like group of species (e.g. *C. phaenopyrum, C. marshallii, C. viridis, C. brachyacantha*) of forest, often river and swamp-forest, margins, whereas the other is the more sand-plain habitat characterised by the sect. *Flavae.* It should be noted that sect. *Flavae* are trees and shrubs that appear relatively shade-intolerant like their more northern relatives. In cold, semi-arid areas (central Asia, central United States cordillera—see Figs. 20, 21, 23a, 23b) there is a virtual hiatus of *Crataegus,* indicating little success in exploiting these habitats. However, western Eurasia has developed a section (*Azaroli*) adapted to winter rainfall maxima, hot summer, scrub regions whereas no such ecological or taxonomic counterpart exists in North America. Two critical species—*C. scabrifolia* of Yunnan and *C. mexicana* of Mexico-Guatemala—are small trees, with thorns of indefinite growth, narrow, barely lobed leaves and large pink to yellow fruit. These occur in similar latitudes (about 20° to 30°N) and broadly similar climatic regions at the southern edge of *Crataegus* distribution. We will return to these apparent vicariants later.

The regions occupied by the infrageneric taxa discussed are shown on the map (Fig. 27).

CHARACTER STATE POLARITY AND OUTGROUPS

The maloids (x = 17) are a natural subfamily of Rosaceae whose fruit is a pome in which a fleshy hypanthial wall overlaps and often closes over the carpels during fruit development. Sterling (1964), in discussing rosaceous carpellary anatomy, agrees that *Crataegeae* are a natural

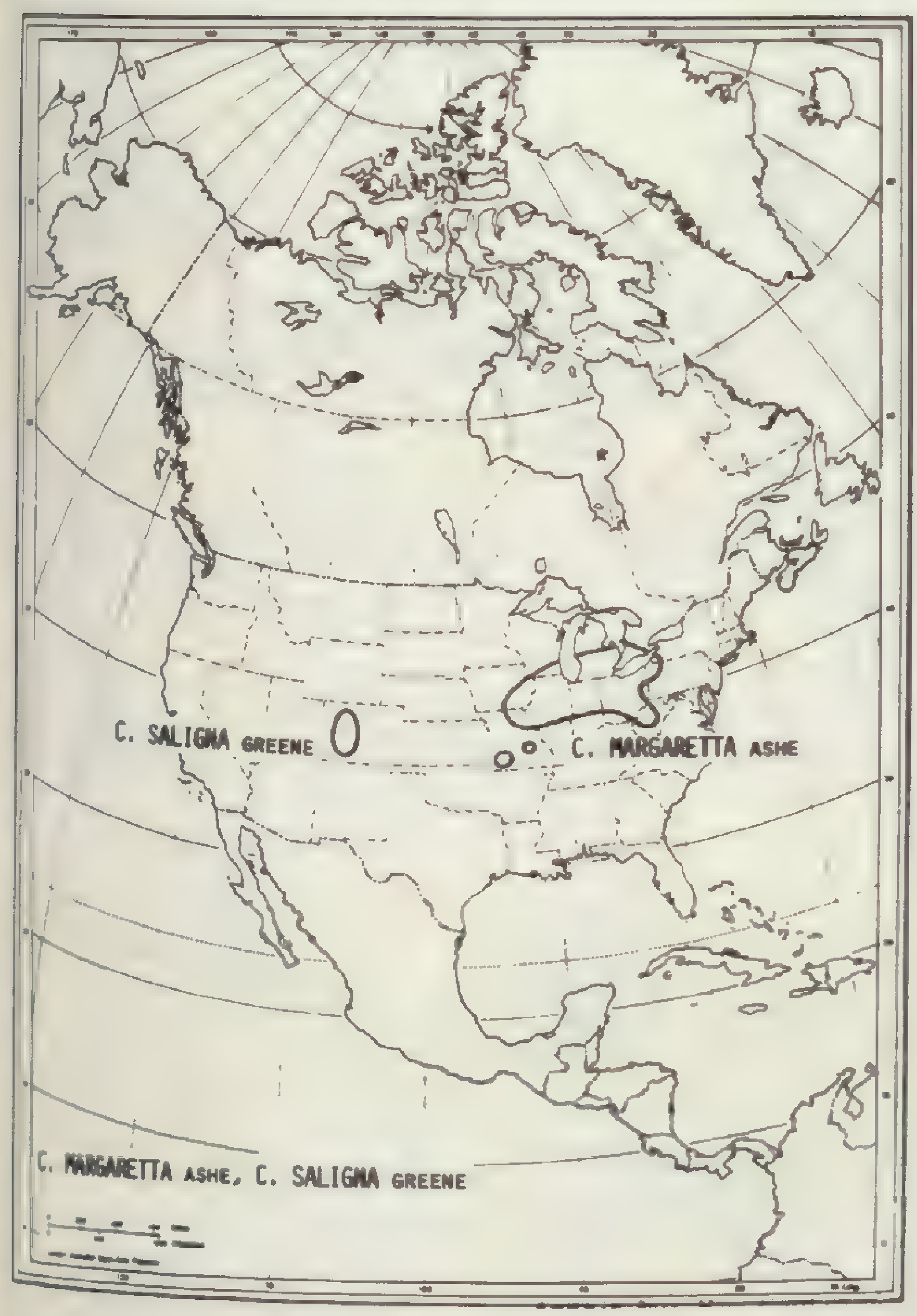


FIGURE 16. Distribution of *Crataegus*: *C. saligna* Greene, *C. margaretta* Ashe.

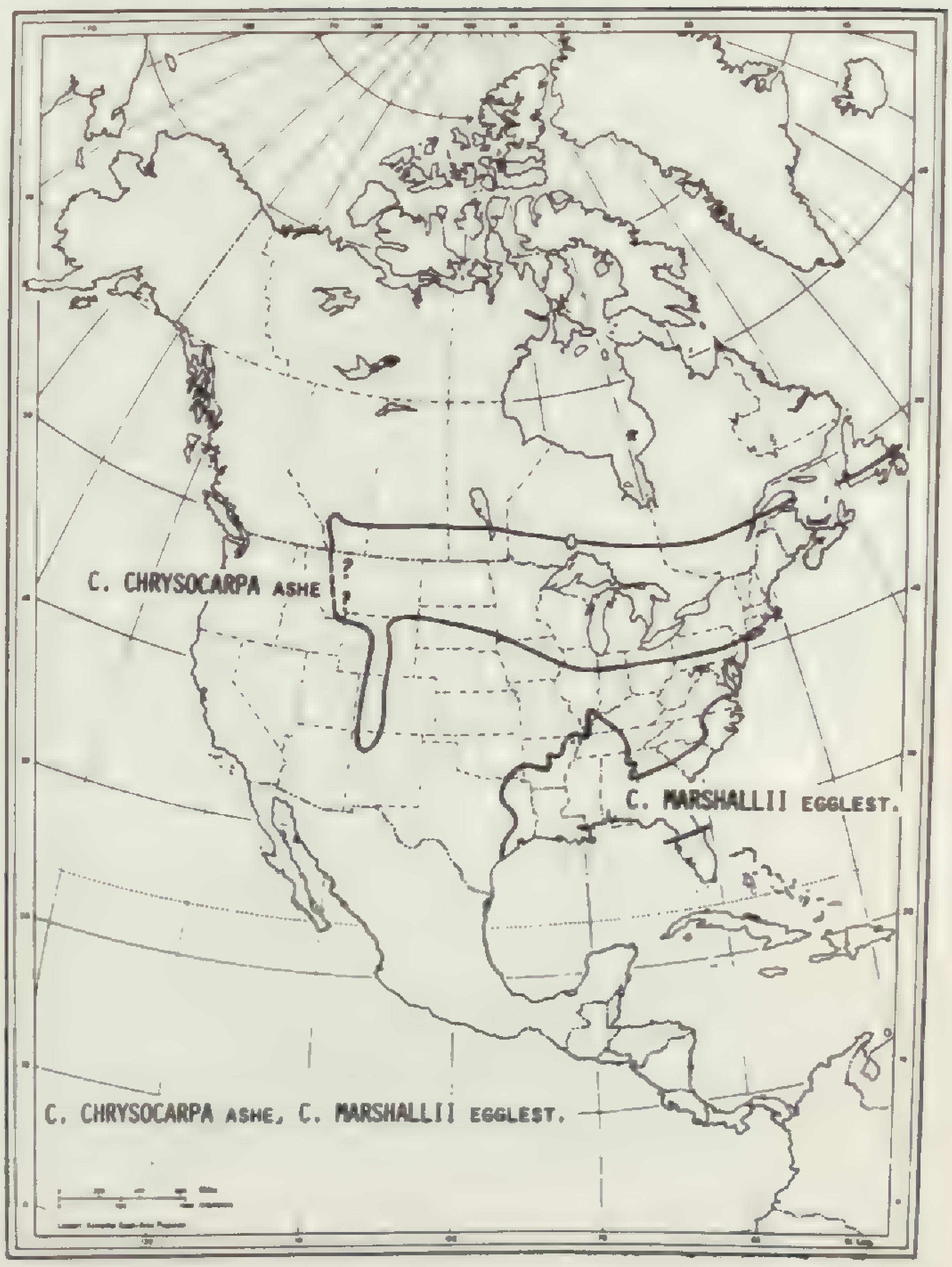


FIGURE 17. Distribution of *Crataegus*: *C. chrysocarpa* Ashe, *C. marshallii* Egglest.

group. The crataegean genera, *Crataegus, Pyracantha, Cotoneaster, Hesperomeles, Osteomeles,* and *Mespilus* were used for outgroup analyses.[3] Crataegean characteristics (Table 8) are tendency to thorniness, small leaves, small flowers in corymbs, generally small fruit with relatively thin hypanthial wall, and bony exocarps generating pyrenes. *Mespilus* is the most distinct genus and differs strongly from other maloids in having much larger leaves and a single-flowered, large-flowered inflorescence on elongating shoots of the current season. However, it produces well-known intergeneric hybrids and a graft-chimaera with *Crataegus*, which are discussed by Byatt et al. (1977). Indeed, intergeneric hybrids are numerous in Maloideae (Fig. 24) although few of these occur in nature. Maloidean genera outside *Crataegeae* differ in numerous characters of habit, thorniness, evergreen-ness, gross leaf-morphology, resting bud, inflorescence (many characters), and striking characters of the development of the fruit. Mere reference to *Chaenomeles, Cydonia, Malus, Pyrus, Sorbus, Photinia, Amelanchier, Raphiolepis,* etc. will underscore this.

It is not immediately clear, on a phenetic basis, which of the *Crataegeae* is the best genus to use as a sister group and, indeed, caution is advised due to the potential for hybridization in the subfamily and the possibility that this existed in creating ancestral *Crataegus*. The phenetic-biogeographic patterning within *Crataegus* as demonstrated earlier argues for substantially long isolation of major sections of the genus and the difficulty of Eurasian-North American migration unless evidence for widespread extinctions is verified. Indeed this is true for the Maloideae as a whole and very much so for the *Crataegeae* (Fig. 25).

The small Andean genus *Hesperomeles,* for instance, with one or two species in Costa Rica-Panama, is related to the main core of the *Crataegeae*. However, it is not very diverse and represents the only native southern hemisphere maloid. It has a specialized distribution (pygmy cloud forest and rocky outcrops at ca. 3,000 m). It is most parsimoniously derived from other *Crataegeae* as a relictual genus tenaciously holding a specialized niche but somewhat anciently crossing Beringia with a rapid move south coin-

[3] *Dichotomanthes* may prove to be crataegean but has a strikingly different fruit.

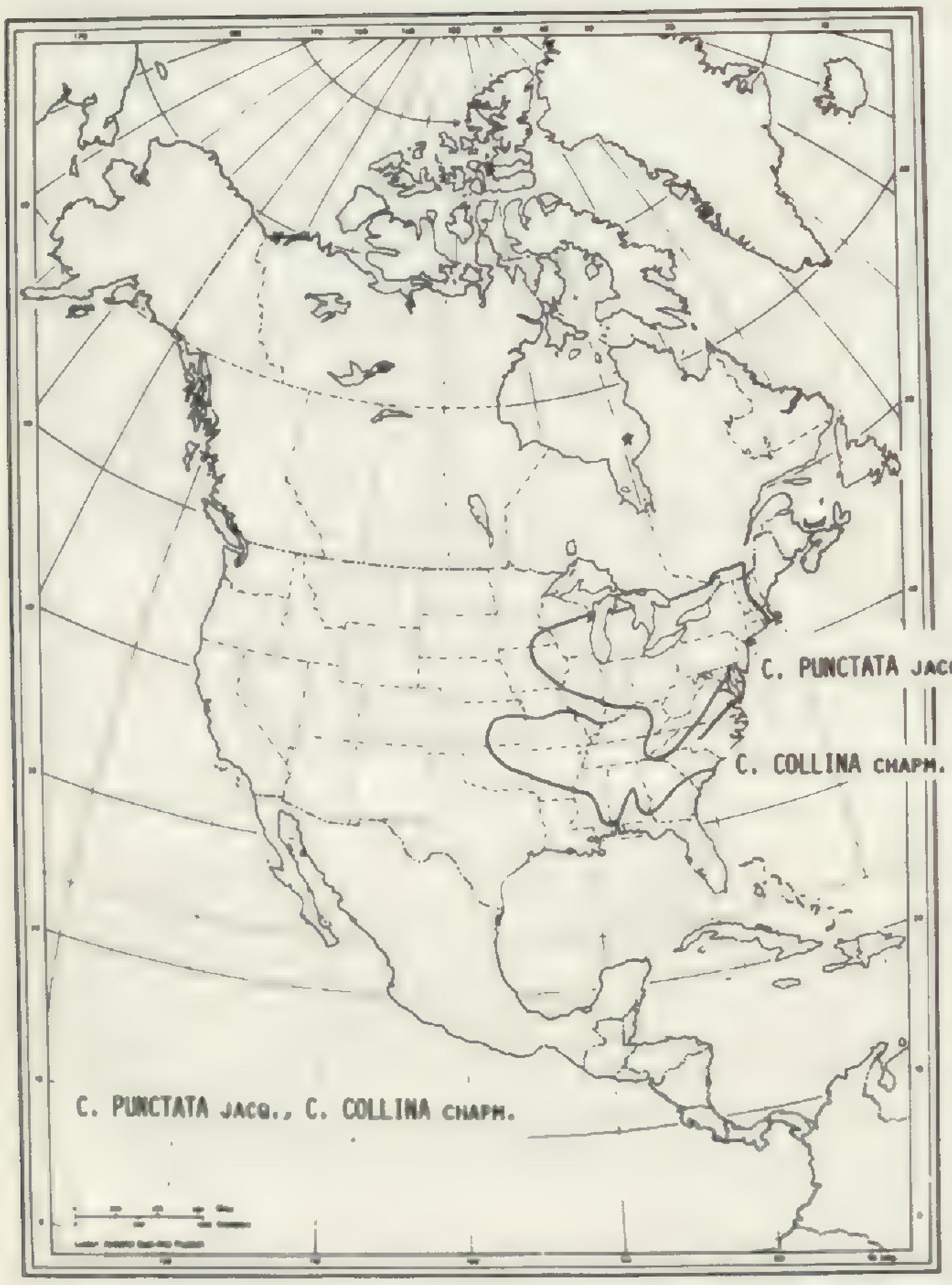


FIGURE 18. Distribution of *Crataegus*: *C. punctata* Jacq., *C. collina* Chapm.

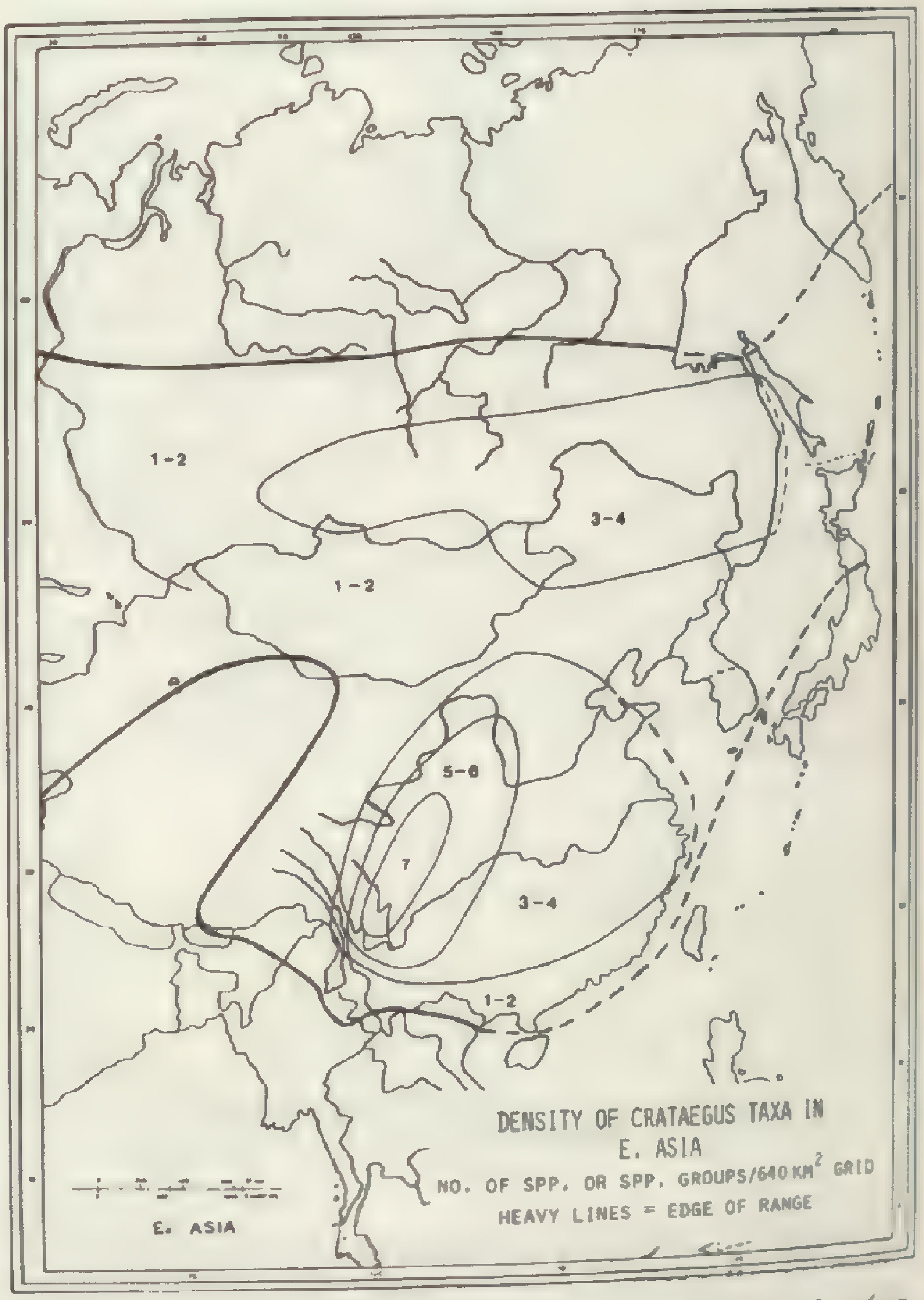


FIGURE 20. Map showing richness of species (no. per 640 km²) in eastern Asia.

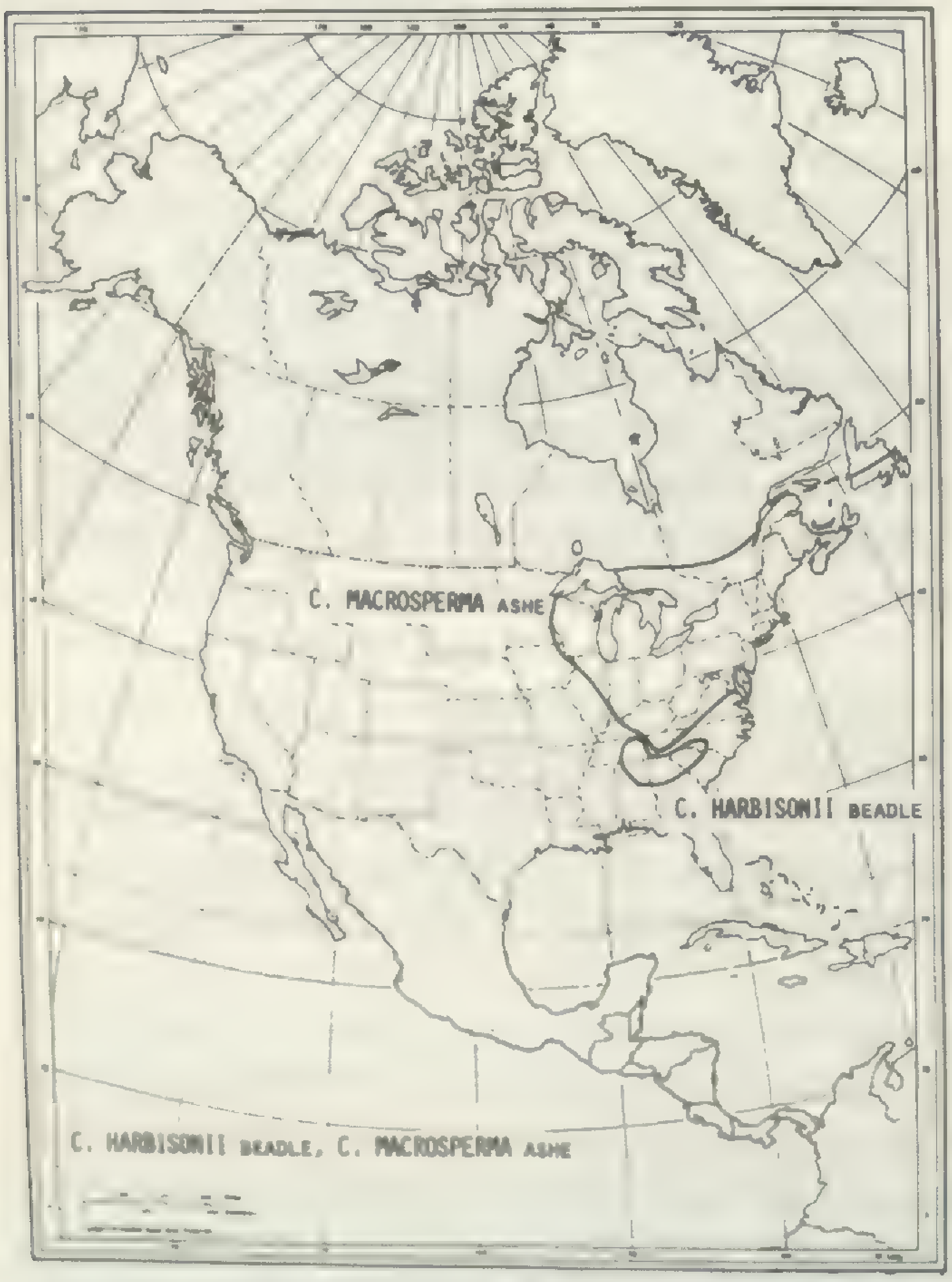


FIGURE 19. Distribution of *Crataegus*: *C. macrosperma* Ashe, *C. harbisonii* Beadle.

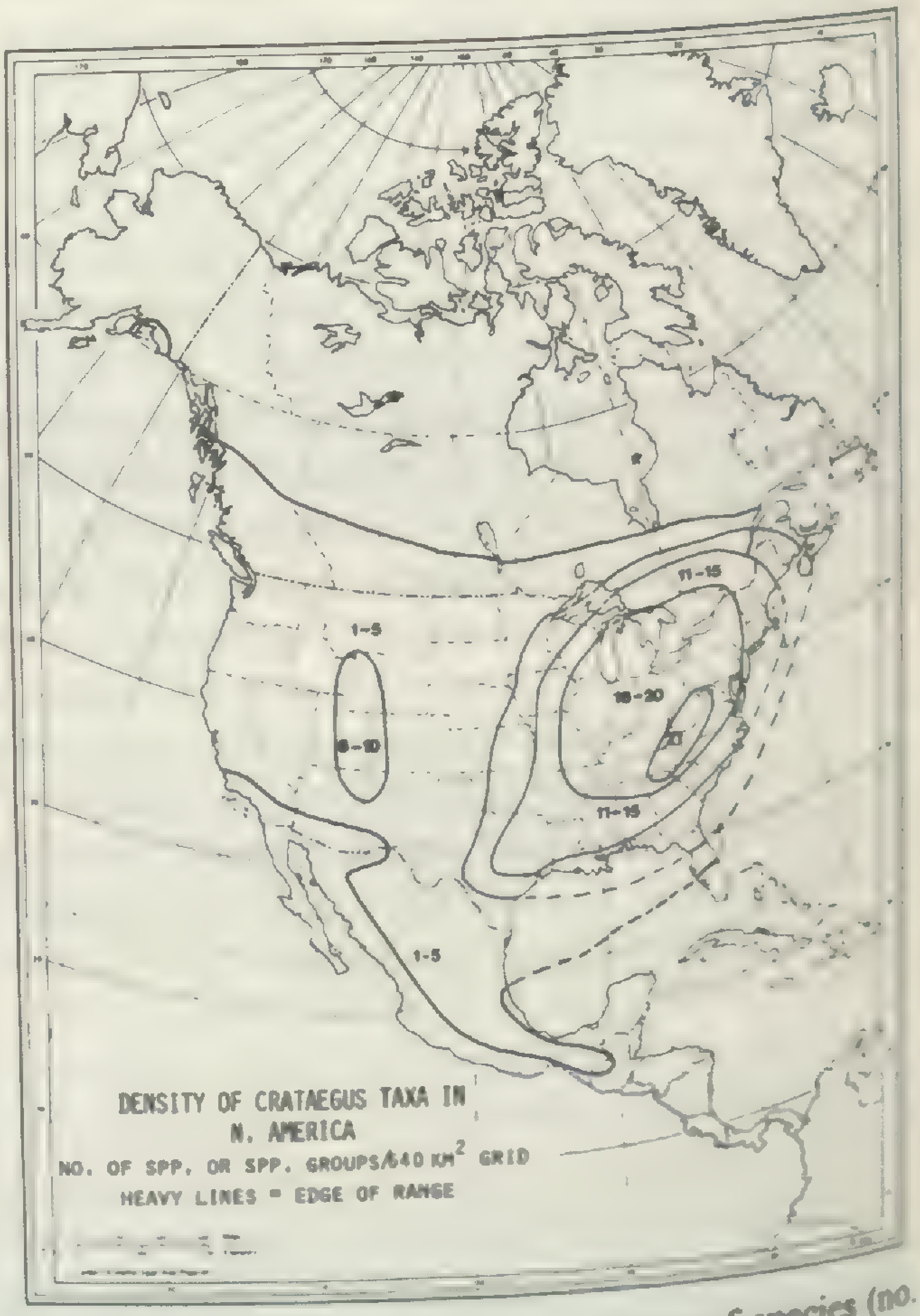


FIGURE 21. Map showing richness of species (no. per 640 km²) in North America.

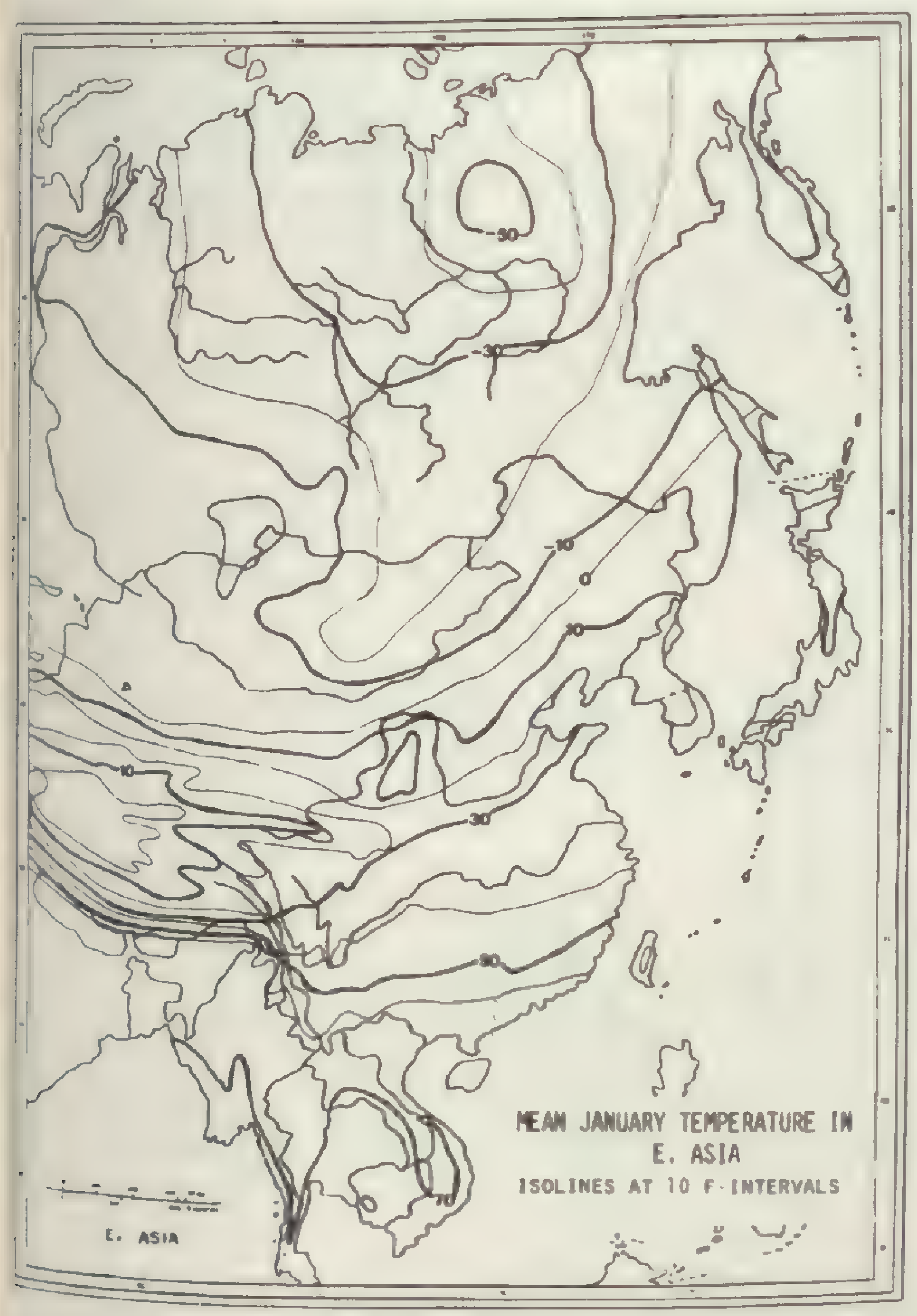


FIGURE 22a. January isotherms. Mean monthly data for eastern Asia. Note 10°F.

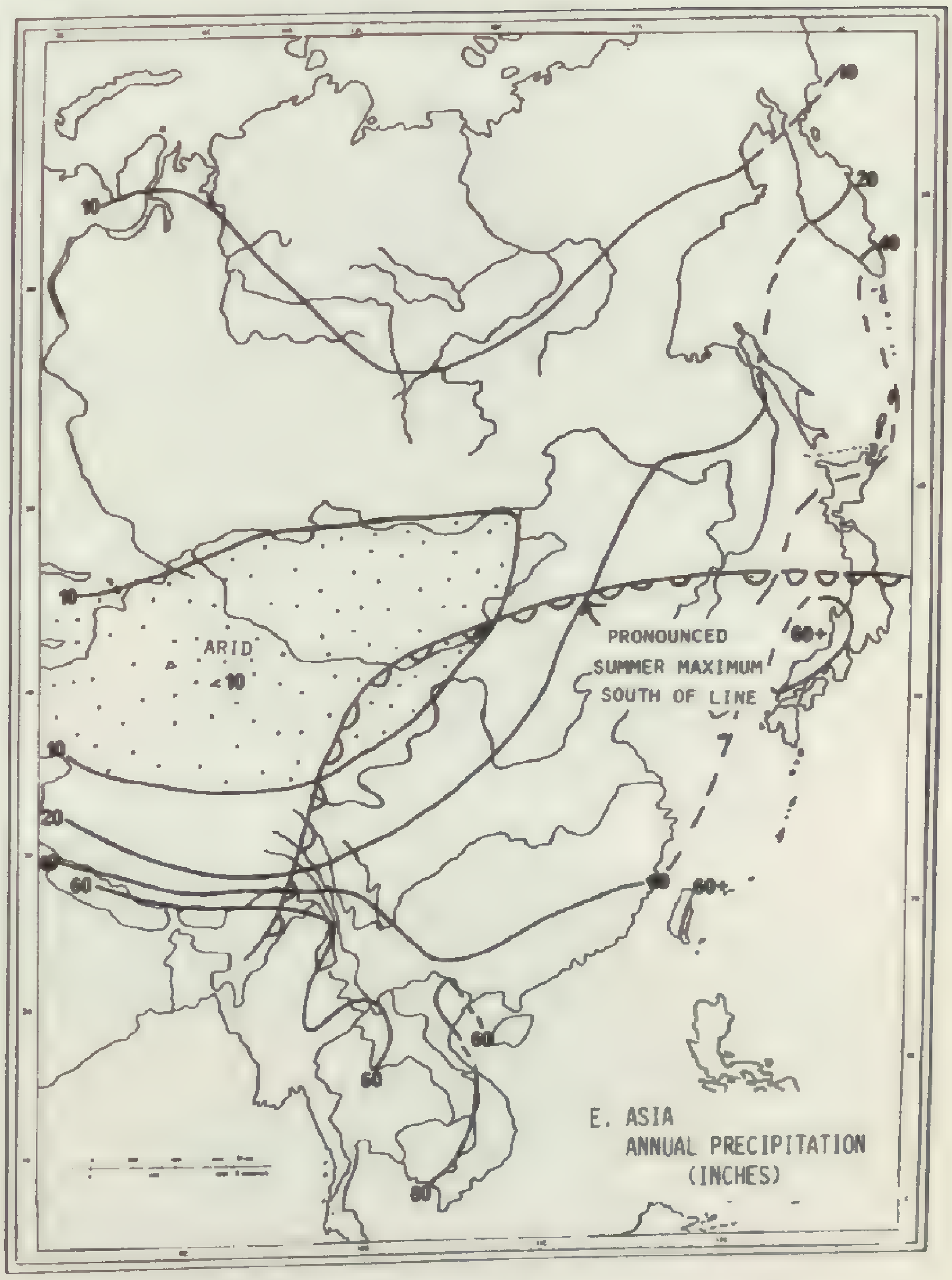


FIGURE 23a. Mean annual precipitation for eastern Asia. Note arid regions and summer maxima.

FIGURE 22b. January isotherms. Mean monthly data for North America. Note 10°F.

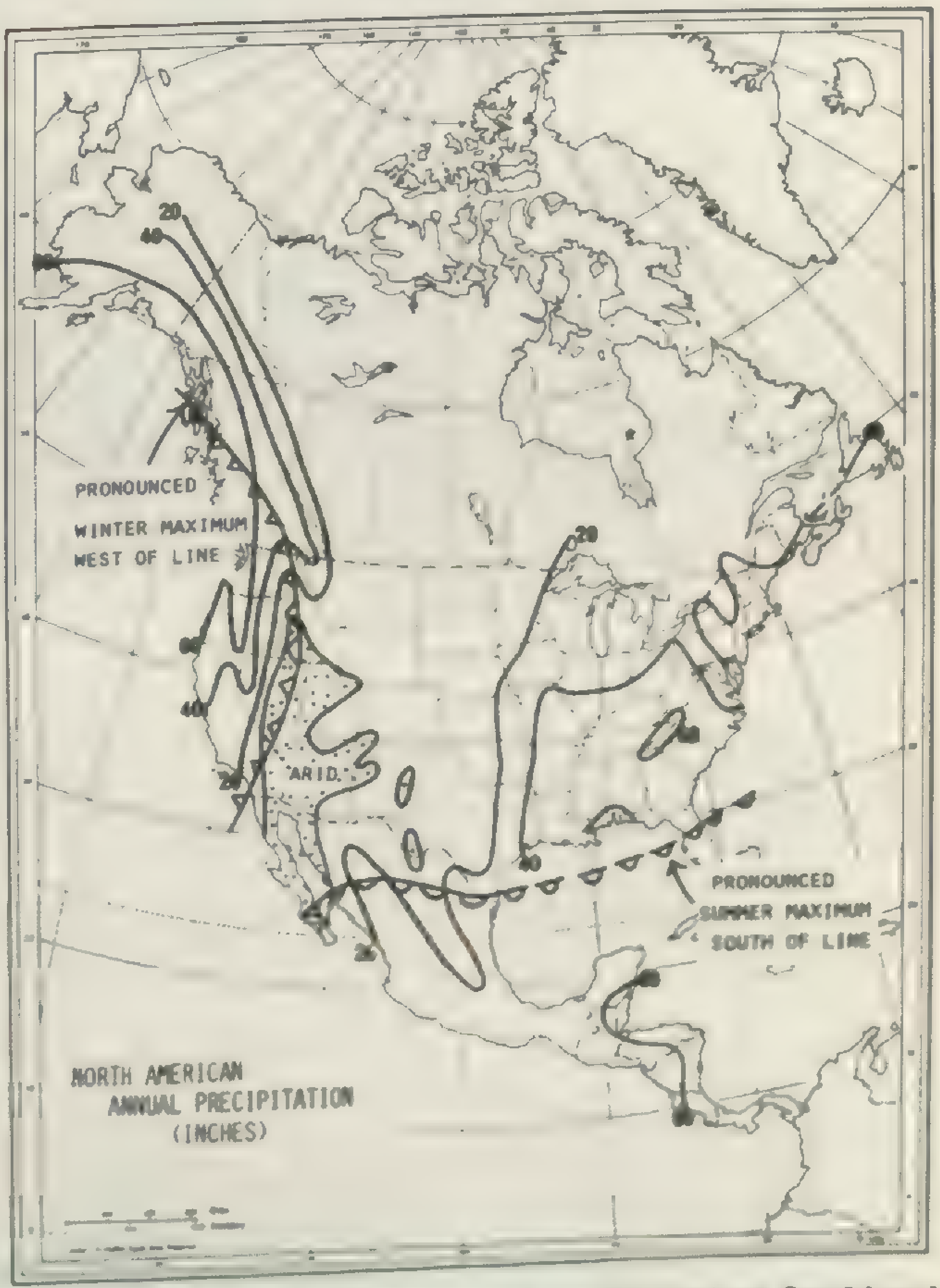


FIGURE 23b. Mean annual precipitation for North America. Note arid regions and winter maxima.

TABLE 8. Technical characteristics of the genera of the tribe *Crataegeae*.

	Habit	Thorns	Leaves	Inflor.	Flowers	Petals	Stamen No.	Pome	Seeds	Others	Distribution No. of Species
Mespilus	small tree	thorny short shoots	simple, large	single, on leafy shoots	large, white	round	30–40	medium; open; brown	5 pyrenes		Europe, W. Asia 1
Crataegus	small shrub to small tree	thorny short shoots or short shoots & thorns	small, unlobed to deeply lobed	corymb	small, white	± round	5, 10, 15, 20	small to medium; sl. open; yellow, red or black	1–5 pyrenes		N. Temp. ≃140
Pyracantha	shrub	thorny short shoots	small, serrate; evergreen	corymb	small, white	± round narrow	20	small; red; closed	5 pyrenes	2 ovule/carpel	Eurasia 9
Hesperomeles	shrub or small tree	shoots, sometimes thorn-tipped	small coriaceous, evergreen	corymb	small, white or pink	round	20	small; red or dark berry	5 pyrenes	1 ovule/carpel	C. & S. America 10
Cotoneaster	small to large shrub	thornless	small, entire	cyme	small, white	± round	20	small; red or black; closed	2–5 pyrenes		Eurasia 100
Osteomeles	tree or shrub	slight tendency to short shoots	evergreen, pinnate	corymb	small, white	irreg. obovate	20	fleshy	5 pyrenes		E. Asia to Polynesia (Hawaii) 3.

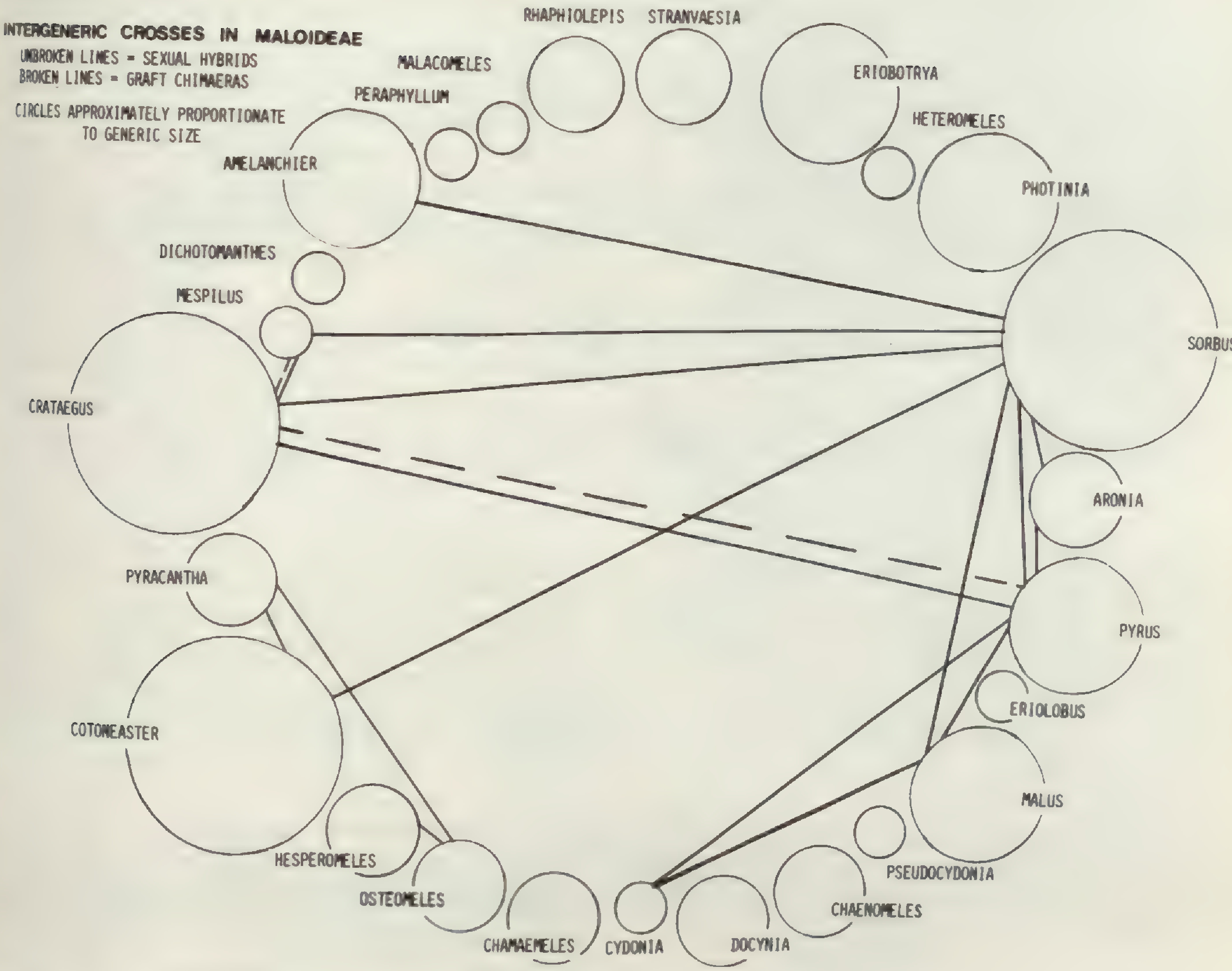


FIGURE 24. Intergeneric crosses recorded in Maloideae (after Robertson, 1974).

cident with a climatic deterioration. A variant of this suggested by D. Axelrod (pers. comm.) will derive *Hesperomeles* from *C. mexicana* or an extinct relative, with similar southward spread. A northward migration to Panama-Costa Rica could be very recent. *Pyracantha*, the other truly thorny *Crataegeae*, has about ten species. It is subevergreen and predominantly warm humid southeast Asian. It is most like *Crataegus*. The non-thorny *Cotoneaster* is a large and quite variable genus widespread in Eurasia, especially temperate Asia. It is not too different from *Pyracantha* but is distinct chemically (Challice, 1981). *Mespilus* is Taurian-Anatolian and is biogeographically, as well as morphologically, well removed from the core of the tribe. It is a candidate hybrid origin genus. The pinnate leaf, specialized habitat, and remarkable distribution of *Osteomeles*, with its Hawaiian disjunction and seashore habitat, permits one to discount it as ancestral.

Pyracantha thus represents the nearest sister group (see also Fig. 26, Table 8) and the biogeographic aspect of adaptive radiation in *Pyracantha-Crataegus-Hesperomeles* is most efficiently postulated from a southwest China base with primitive *Crataegus* emerging in that area, and now being represented only by *C. scabrifolia* (Fig. 27). Diversification to Western Eurasia has probably only occurred once or twice on the basis of present biogeography and the existence of major barriers in Central Asia, and in this one may consider the early Tertiary Turgai Straits. The Beringian route has been available geographically throughout the Tertiary but available climatically only intermittently (Wolfe, 1977), perhaps only in the Eocene, Middle Miocene, and in certain interglacials. The major groups of *Crataegus* are preponderantly different in North America from Eurasia, which together with the diversities in North America itself are clearly indicative of several independent movements Asia to North America via Beringia, followed by southward range collapse in both continental areas.

In general, correlated suites of characters found

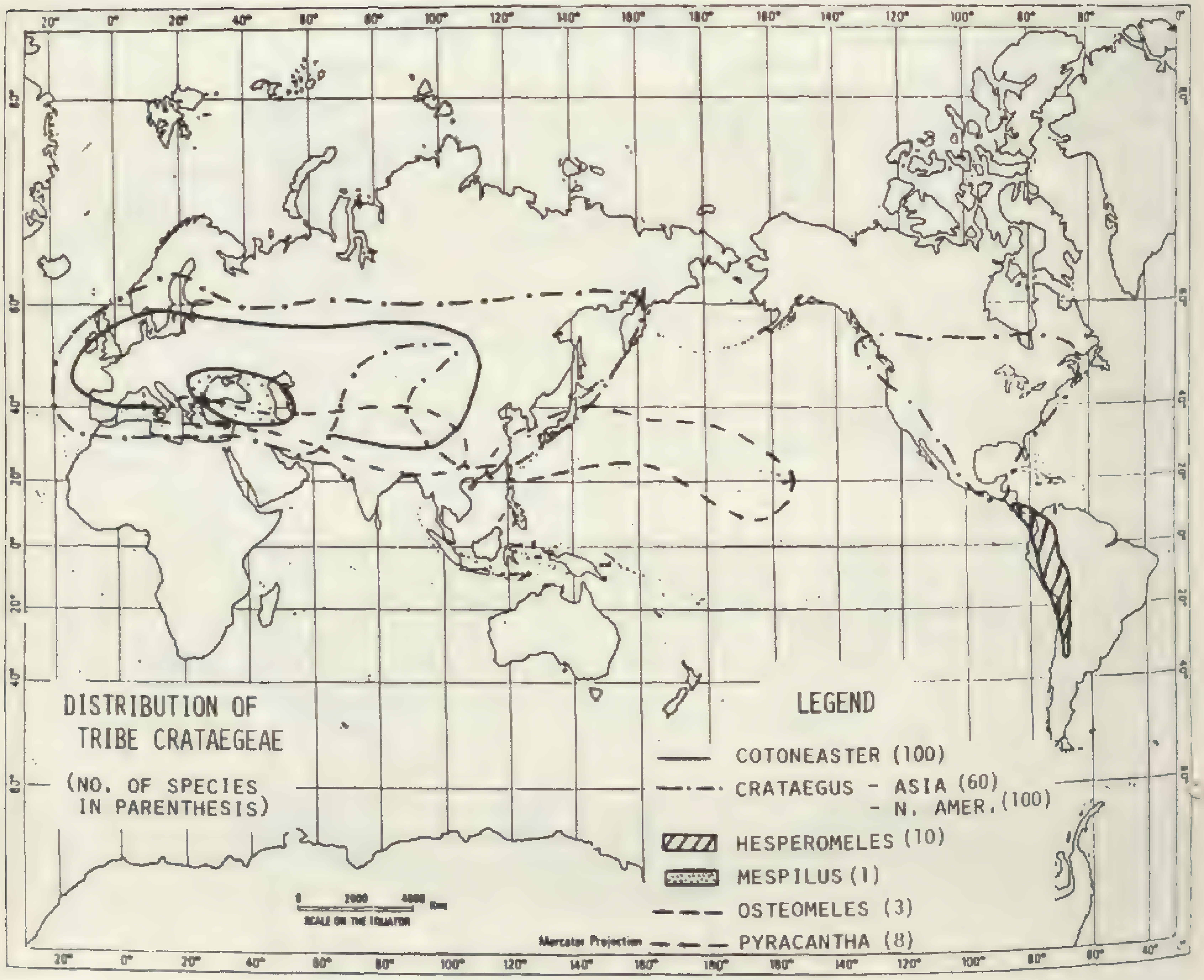


FIGURE 25. Distribution map of crataegean genera.

in the majority of crataegean genera are considered ancestral, and, in cladistic terminology, are symplesiomorphic. Apomorphic states are logically derived. Figures 29 to 31 summarize diagrammatically certain presumptive evolutionary trends in *Crataegus*, and Table 5 presents the total character set used.

Cladistic Results

Figure 28 is a computed pro-cladogram for the 75 OTUs used in the taxonomic work. The target diagram format is used because the cladistic predicates permit apomorphy counts (= advancement indices) and because of spatial requirements (numerous OTUs) on the diagram. Computation was stopped, or the results not plotted, when patristic distance exceeded eight units and where several different fusions of similar parsimony in longer stems (±2 units) were possible. Thus many of the major groups, viz. Chinese and Siberian alliances (including sect. *Sanguineae*), and other American and southeastern United States taxa are not tied into the central core of the genus. However, the critical centre, including *C. scabrifolia* and *C. mexicana*, is tied in. *Azaroli* and *Oxyacanthae*, however, seem relatively reliably connected to the core of the genus.

Therefore, with some exceptions, the cladogram proposed unites only the tightly-knit groups. In doing so, it strongly reflects the phenetic results and it also conforms with the biogeographic results. Nevertheless, to mindlessly push the cladogram through to completion at this stage, in my opinion, would be a fundamental mistake with the relatively few characters polarized. Had it been possible to polarize more characters, some of the ambiguities may well have been resolved. For instance, it is critical to discover whether the '*Americanae*' are best derived from the *Sanguineae*, which would optimize (i.e. generate greater cladistic parsimony), in general, on the development of thorns, of leaf-shape, climatic adap-

tations, etc., or whether a parallel '*Americanae*'-*Sanguineae* evolution took place independently on the two continents. In view of the weak relationship of '*Americanae*' to southeastern United States taxa and to *C. mexicana*, and in view of the fairly numerous Neogene *Crataegus* records (of various leaf shape) from the west of the continent, extra Beringian migrations represent an attractive viewpoint.

However, the pro-cladogram as currently set up does not make the *Sanguineae*-'*Americanae*' connection very attractive; but if the '*Americanae*' were radially raised on the pro-cladogram (=additional synapomorphies) a link from species like *C. kansuensis*, *C. maximowiczii* or *C. aurantia* becomes extremely attractive. In lieu of attempting the difficult task of polarizing a significant extra number of morphological characters, in the short term it is planned to substitute the use of phenolic assays in the clarification of group structure. These data have been found useful in Maloideae by Challice (1981) and Sinnott and Phipps (1983).

Note that as fusions are made between currently unconnected groups on the cladogram this will increase the number of definite homoplasies. Homoplasies have not been counted but are evidently highly numerous, but this is conformable with our biological understandings of *Crataegus* reproductive behaviour.

Another reason for caution in accepting long computed patristic distances lies in the polyploid and hybrid nature of Maloideae. The tribe is of postulated alloploid origin (maloid $x = 17$ from $x = 8 + x = 9$), numerous intergeneric hybrids are known (some in nature) and some involving *Crataegus* (notably with *Mespilus*) while proven and plausibly suspected hybridization in *Crataegus* is frequent (Phipps, 1984). Thus, long patristic unions as computed in standard programs might totally override and obscure actual hybridization events. This reinforces the rationale for leaving the published situation at the developmental stage of the pro-cladogram in 1982 until new data are analyzed.

Dispersal Ability

Pomes of *Crataegus*, as well as those of other similar berry-like fruit about 1 cm size, are commonly considered to be bird-dispersed (Phipps & Muniyamma, 1980). If this is so, then the potential for long-distance dispersal (LDD) immediately becomes a prominent consideration.

FIGURE 26. *Pyracantha crenulata* (lower), *Crataegus mexicana* (top left) and *C. scabrifolia* (top right) compared. Note leaf-shape and spiny short-shoots.

What is remarkable, however, is the paucity of hard data on *Crataegus* dispersal (e.g. DeBoer, 1979). Information, such as it is, is related to what eats *Crataegus* berries, and not how far seeds may travel in the gut of the fructivore. There is no question that several species of passerines and game birds eat *Crataegus* fruit. They may also do so in the autumn, while on migration. Birds during migration may lose course, due to navigation problems or by being storm driven. Numerous records attest to such birds ending up on the 'wrong' side of the Atlantic or Pacific Oceans. However, were such LDD to be a significant cause of *Crataegus* distribution patterns then it is inferred that taxonomically like kinds of *Crataegus* would be more commonly found than is actually the case on opposing sides of the major northern oceans. Indeed, the explanation of the distribution of only southeastern United States *C. marshallii* (related to ser. *Oxycanthae* of Europe), and possessing the smallest size of *Crataegus* fruit (3 × 6 mm), is aided by LDD concepts for a parsimonious explanation of its location. The extreme differences between the North American and European *Crataegus* floras indicate the effective closure of Atlantic route to

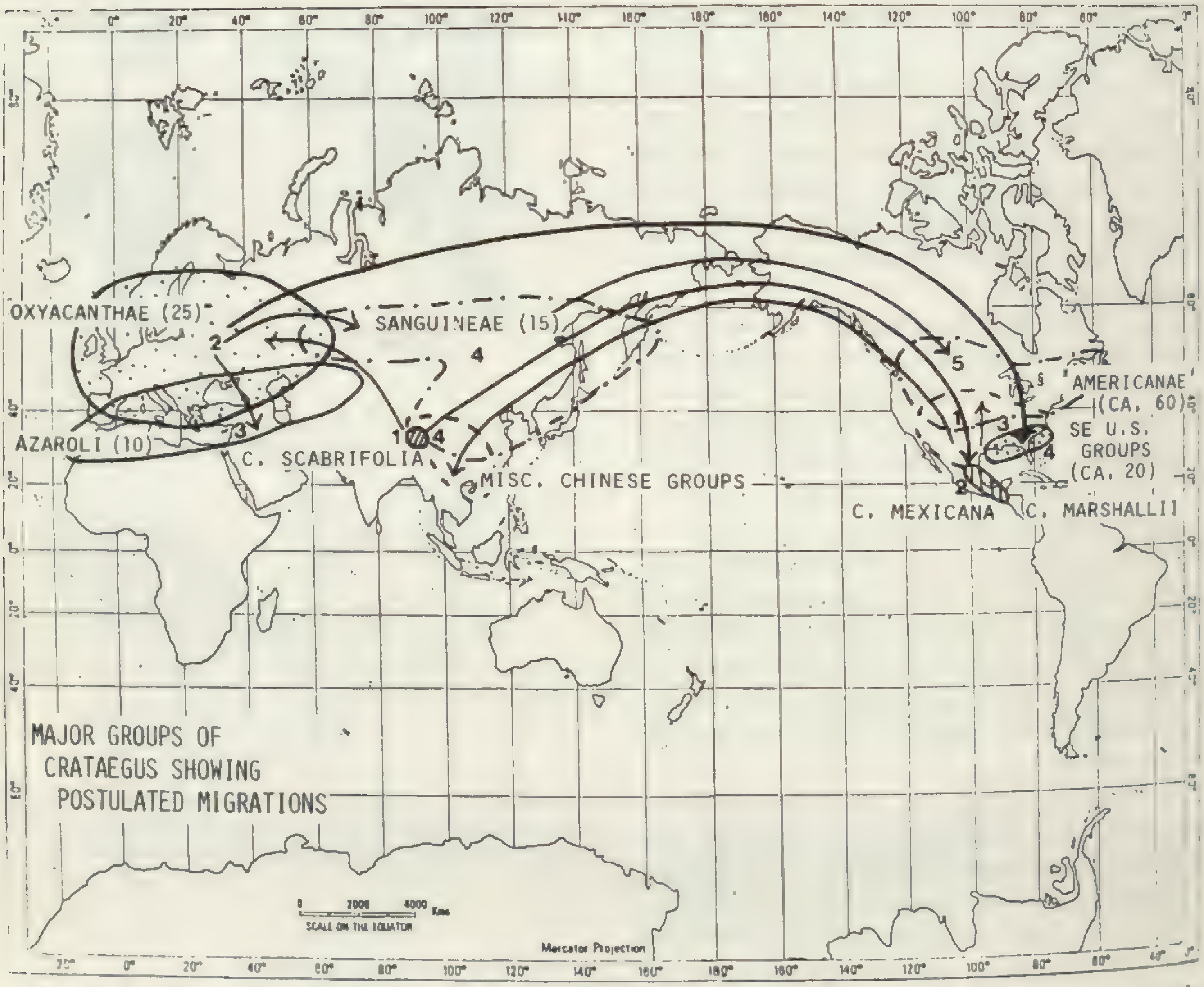


FIGURE 27. Major groups of *Crataegus* showing postulated migrations. Non-bracketed numbers trace the sequence.

Crataegus during most or all of *Crataegus* evolution. In view of the Atlantic situation, the East Asian-American taxonomic differences, and with the avian potentials being essentially equivalent, LDD across the Pacific must also be stochastically discounted. Both ungulates and rodents eat *Crataegus* fruit and seeds but they can hardly be agents of LDD.

Thus, short-distance dispersal (SDD), the effects of which are abundantly observed in nature, for instance in the rapid establishment of new *Crataegus* populations, is certainly adequate to explain dispersal and radiation between the two northern continents. Short-distance dispersal through Beringia thus remains the only serious candidate migration route and it is proposed as occurring whenever the Beringian climate permitted *Crataegus* to migrate to and thrive in the Chukchi-Alaska region.

PALEONTOLOGICAL CONSIDERATIONS

The Alaskan-Asian contact in Beringia has remained essentially unchanged geographically, from the standpoint of this paper, since the early Tertiary. Rotation of plates on an Alaskan fulcrum, terrane accretion, etc., are of great interest to geologists but of less significance to this study. The sea gap, however, is of more consequence, and its exact extent in Beringia through the Tertiary is apparently not easy to establish. The consensus, however, is that it was usually narrow and with or without intervening small islands it has probably been a negligible SDD barrier throughout. Sea-level fluctuation through the Pleistocene must certainly have varied the width of this barrier and could have been one of the factors that affected timing of any Pleistocene *Crataegus* SDD. Clearly, however, the critical factor for the Beringian route is paleoclimate.

It is, therefore, posited that during climatic optima there is no significant barrier to American or east Asian *Crataegus* approaching Beringia using SDD. The Tertiary and Quaternary paleoclimate of Beringia are, therefore, of some interest. Firstly, Beringia has been at high latitudes throughout the Tertiary. Indeed, during the

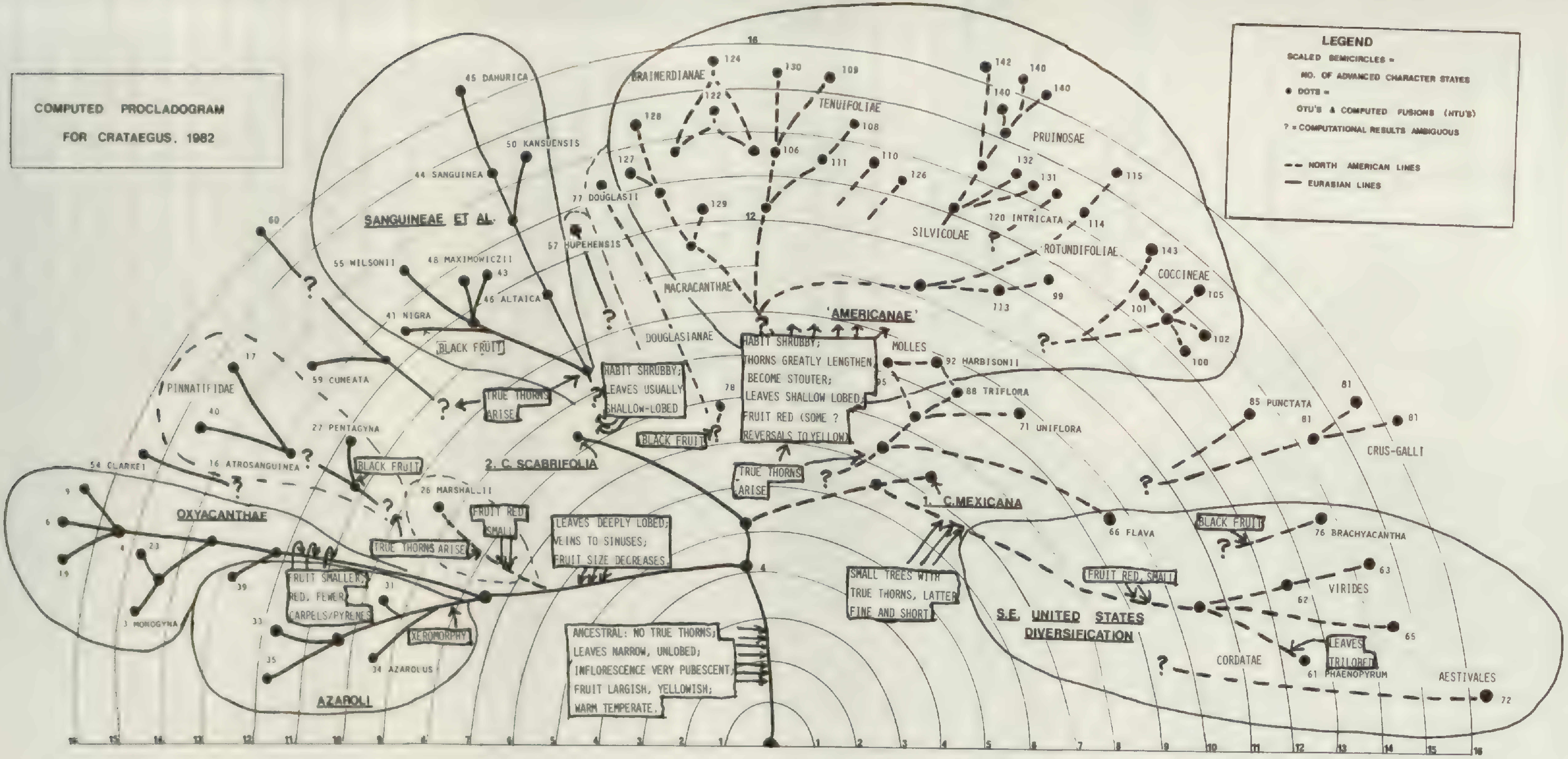


FIGURE 28. Pro-cladogram of 75 species of *Crataegus* based on 18 characters. (OTU numbers cross-referenced to Appendix A.)

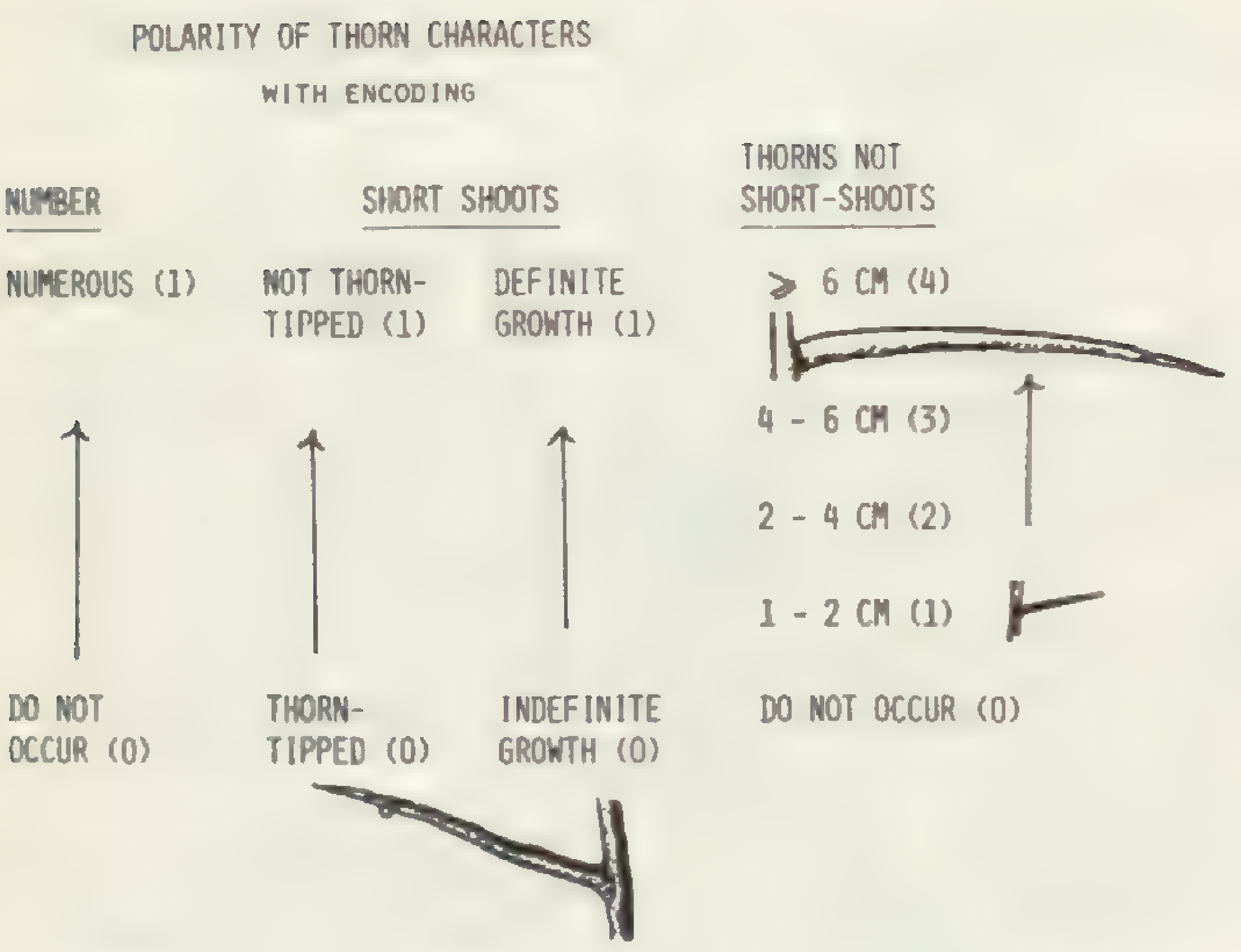


FIGURE 29. Diagrammatic representation of polarity in *Crataegus* characters: (a): thorn.

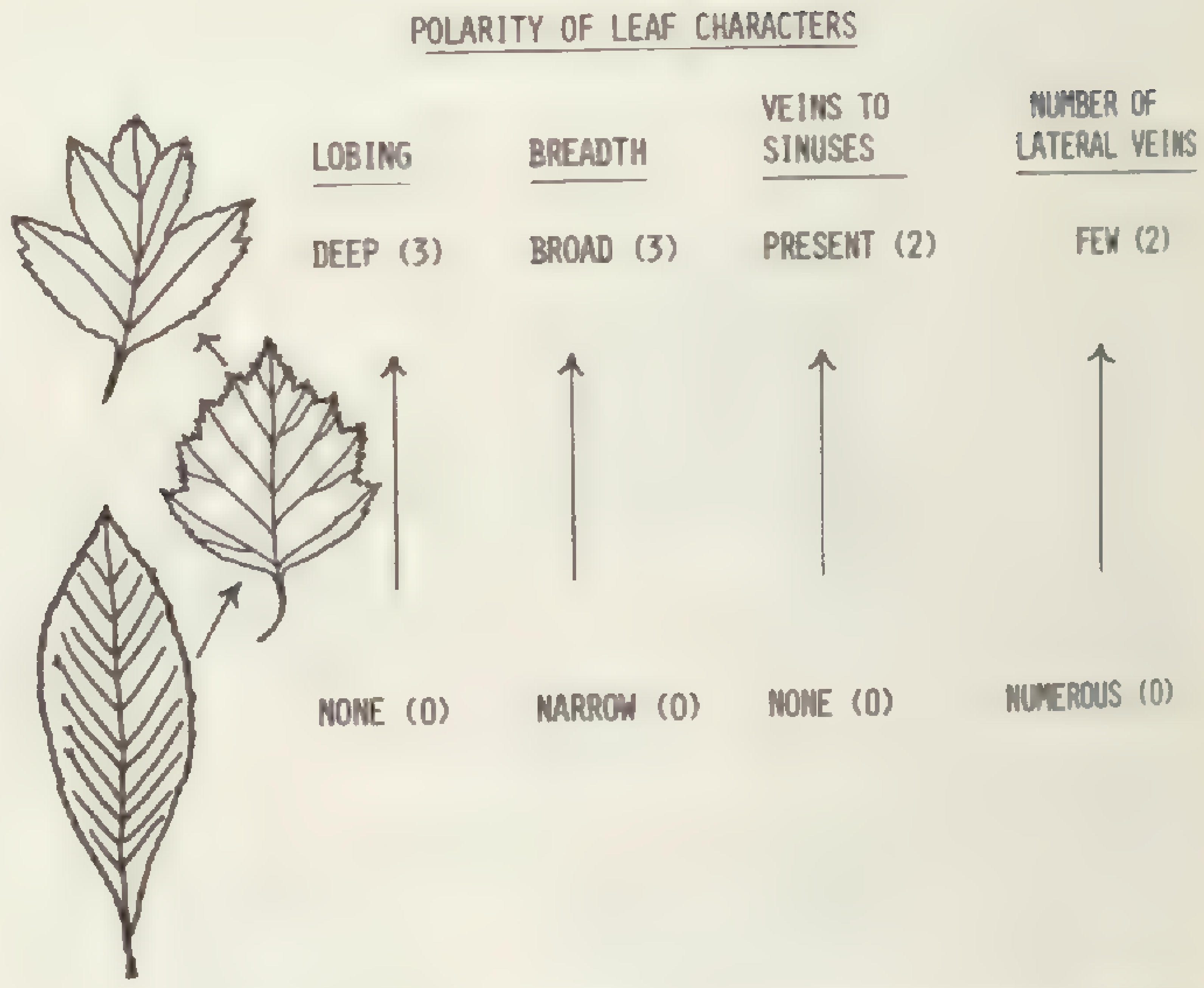


FIGURE 30. Diagrammatic representation of polarity in *Crataegus* characters: (b): leaf.

Eocene, the North Pole was in the (present) Chukchi Sea. Data on northern Hemisphere climate changes, however, indicate optima in the Eocene, middle Miocene, and possibly, certain interglacials (e.g. Lamb, 1977). The northern limits of extant *Crataegus* are, however, well to the south of Beringia, and these seem to be cold-hardy, phyletically advanced species (e.g. *C. sanguinea, C. aurantia, C. maximowiczii, C. chlorosarca, C. altaica* (Asia), and *C. douglasii, C. chrysocarpa* (N. America)).

It is inferred, therefore, that *Crataegus* crossed (and perhaps re-crossed) Beringia a limited number of times, during climatic optima. The Alaskan warm-climate interludes are well discussed by Wolfe (1971, 1977). A possible scenario is:

a) *Eocene event*

Ancestral *Crataegus* to Beringia, followed by range collapse southward on both continents with the vicariants *C. mexicana* becoming an ancient relict now settled in Mexico and *C. scabrifolia* in Yunnan.

b) *Miocene event*

Ancestral sect. *Sanguineae* types, e.g. *C. maximowiczii* types to Beringia, likewise followed by range collapse southwards and extensive radiation of ancestral and descendant taxa on both sides of the Pacific.

Fossil benchmarks would help secure the dates in question, as would a more detailed knowledge of Beringian paleoclimate. Nevertheless, it would seem that substantial time intervals are required to permit the degree of evolution observed. A telescoping of the proposed time-scale is possible as long as event (a) is not much later than Miocene on general evolutionary considerations.

FOSSIL BENCHMARKS

Fossil benchmarking appears to require a critical re-evaluation of all proposed *Crataegus* fossils. It is noteworthy that some for-a-period well-accepted *Crataegus* have been transferred to genera as taxonomically unrelated as *Alnus* (e.g. Wolfe, 1971). However the collected works of reputable palentologists (e.g. Chaney, 1927; Lamotte, 1936; Oliver, 1936; MacGinitie, 1934; Wolfe, 1977) etc. are bound, in the opinion of this author, to yield a number of genuine *Crataegus* records at least as far back as the Oligocene. Indeed, the unique leaf morphology of some *Crataegus* makes it certain that some existing records are correctly attributed to *Crataegus* if indeed, they match extant genera. Projection back to the Eocene (e.g. Lamotte, 1952) is far less secure and this period possibly saw the origin of Maloideae.

DISPERSAL OF OTHER MALOIDS

Of the maloidean genera only five (*Crataegus, Sorbus* [only subg. *Aucuparia*], *Malus, Amelanchier,* and *Photinia*) occur in both northern macrocontinents (Table 9). While the fruits of *Chaenomeles, Cydonia,* and some others are large, in general maloid pomes are small (about the same as *Crataegus* in variability). Their patterned distribution likewise must surely indicate either very modern evolutionary diversification in the whole tribe or poor LDD. Obviously the latter hypothesis conforms best to the *Crataegus* argument. Indeed for the entire Maloideae, LDD explanations are cogent for only three species—*Cratae-*

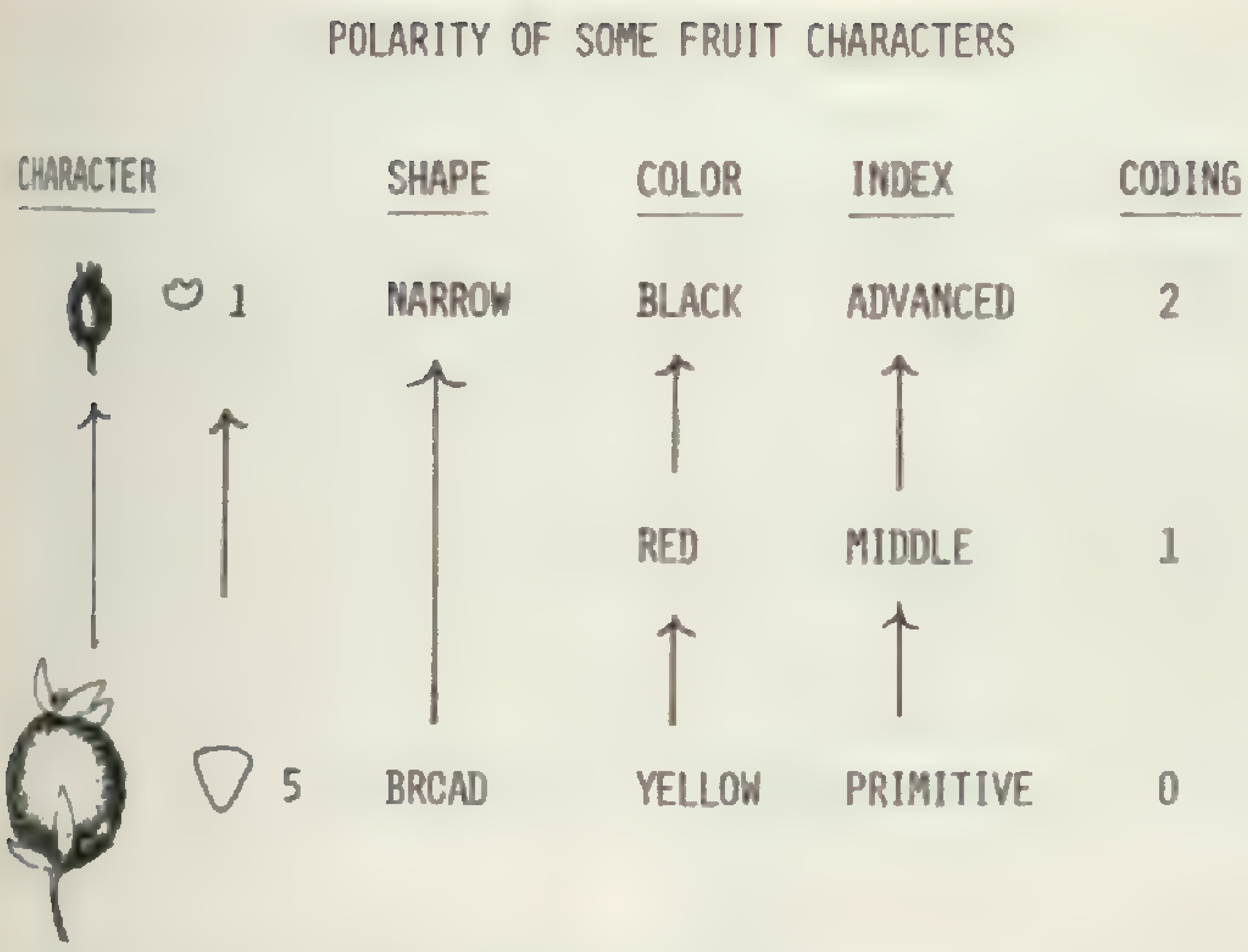


FIGURE 31. Diagrammatic representation of polarity in *Crataegus* characters: (c): fruit.

gus marshallii, *Chamaemeles coriacea* (endemic to Madeira), and *Osteomeles anthyllidifolia* (Hawaii) although this latter, disjunct from eastern Asia, could have an anthropogenic explanation.

Taxonomy of United States *Crataegus*

The wide variety of apparently not closely-related forms restricted to the southern United States (e.g. *Microcarpae, Aestivales, Virides, Flavae, Brevispinae*) is indicative of a relictual flora that had diversified long in the past. The above groups offer little parallel to Asiatic forms except for hypothetical symplesiomorphies between *Virides* and *C. hupehensis*. The weak relationships between southern United States groups and other North American forms, e.g. '*Americanae*,' *C. crus-galli*, and *C. mexicana* has already been noted. It is fascinating to be able to postulate a group of southeastern United States relicts.

Taxonomy of Chinese *Crataegus*

Most Chinese species are fairly closely interrelated, in two subgroups, the northern *Sanguineae* alliance and the slightly more southern *kansuensis* alliance. It is these two sub-groups that relate most closely to North American *Crataegus* in the group '*Americanae*.' *Crataegus cuneata* of southeastern China, however, is very distinct from other Chinese taxa, as is *C. hupehensis*, this plant having a remarkable leaf-shape and appearing to be thornless, whereas *C. scabrifolia* is quite unlike other Chinese species as already discussed. These last two probably represent old phylads, *hupehensis* perhaps representing the only east-west Beringian *Crataegus* migration. *Crataegus tangchungchangii* is inadequately known.

TABLE 9. Listing of maloid genera geographically (showing numbers of species per genus).

	Euras.	Am.
Tribe Crataegeae		
Mespilus (1)	1	—
Crataegus (150)	55	95
Pyracantha (8)	8	—
Hesperomeles (9)	—	9
Osteomeles (3)	3	—
Cotoneaster (100)	100	—
?*Dichotomanthus*	1	—
Tribe Sorbeae		
Docynia (5)	5	—
Chaenomeles incl. *Pseudocydonia*	5	—
Cydonia (1)	1	—
Malus (45)	40	5
×*Malosorbus* (1)	1	—
Eriolobus (1)	1	—
Pyrus (45)	45	—
Eriobotrya (30)	30	—
Photinia (50)	45	5
Heteromeles (1)	—	1
Stranvaesia (6)	6	—
Rhaphiolepis (8)	8	—
Sorbus (125)	120	5
Aronia (3)	—	3
Chamaemeles (1)	1	—
Amelanchier (18)	6	12
Malacomeles (2)	—	2
Peraphyllum (1)	—	1

Summary

Phenetic and biogeographical analysis shows a very strong patterning of *Crataegus* species-groups in regions. Among these, *Azaroli* and *Oxyacanthae* of Europe and Western Asia are particularly distinct. The Siberian sect. *Sanguineae* and allies have much in common with North American '*Americanae*' in spite of usually separating slightly when subjected to numerical taxonomic analysis. In the United States and Canada a varied group of southern species distinguish rather well from the more northern '*Americanae*' species. Apparent vicariants *C. scabrifolia* and *C. mexicana*, without true thorns, occur in Yunnan and Mexico respectively.

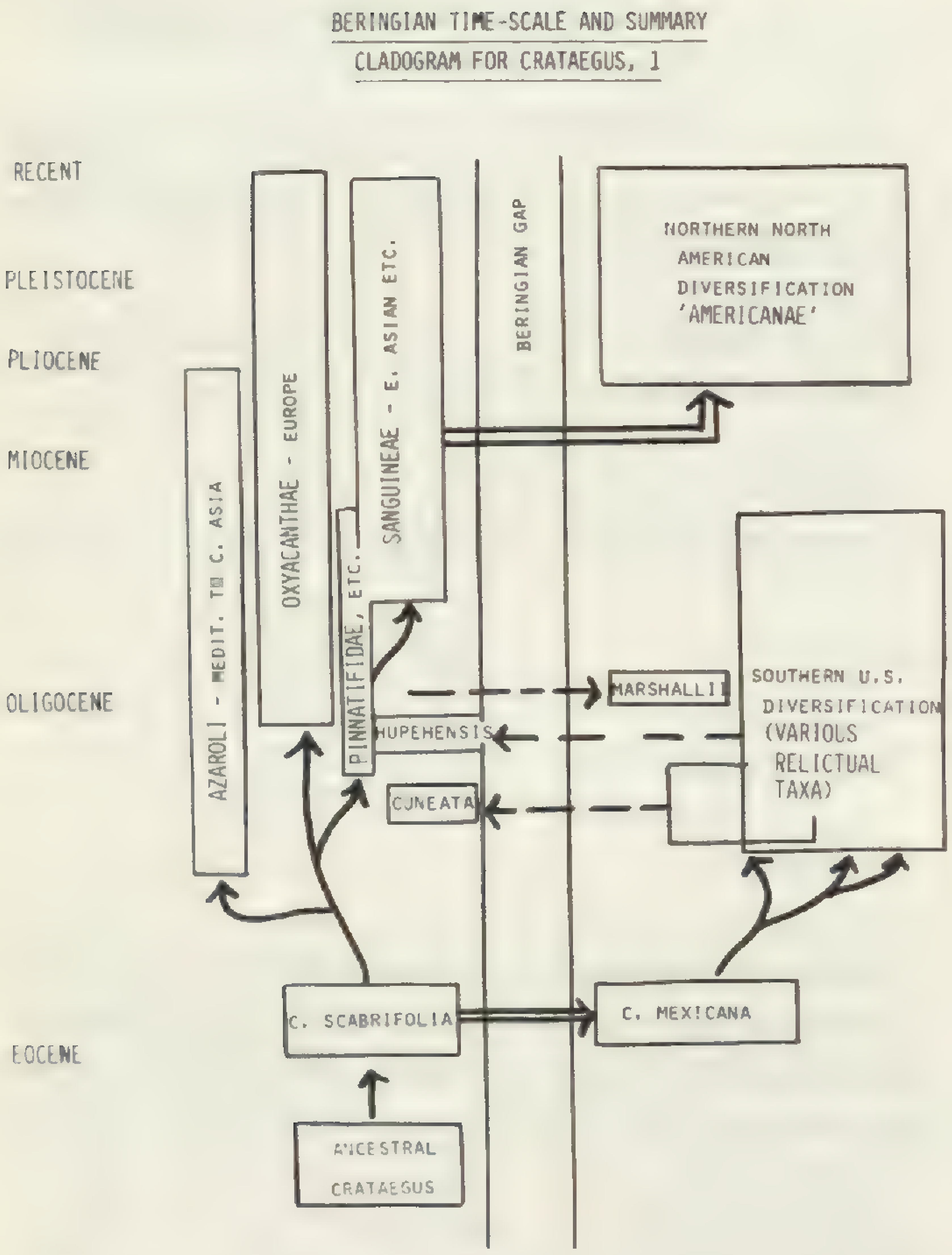


FIGURE 32. Simplified vicariance cladogram illustrating preferred theory (see text for fuller explanation).

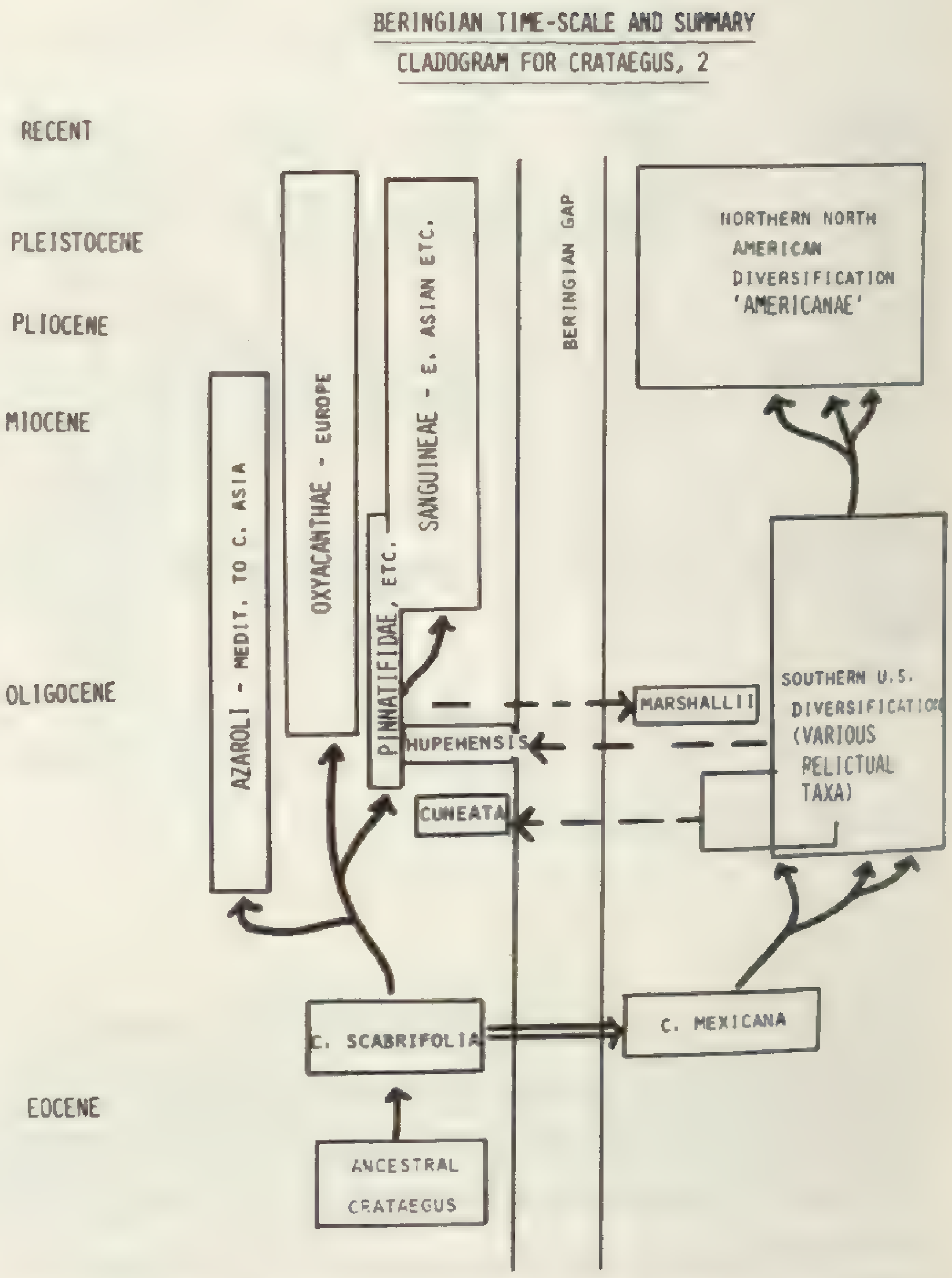


FIGURE 33. Simplified vicariance cladogram illustrating alternative hypothesis (see text for fuller explanation).

Cladistic analysis is based on generating plesiomorphies from the natural tribe Crataegeae and indicates remarkable similarities between *Pyracantha, C. scabrifolia,* and *C. mexicana.* The cladistic algorithm was not pursued to completion due to ambiguities about how major groups might be connected. These ambiguities are reinforced by knowledge of potential for wide hybridization among Maloideae and also, specifically, within *Crataegus.*

Biogeographical thinking is thus brought into the cladistic argument, the reasoning resting strongly on the very low likelihood of LDD. The few plausible LDD events are noted. This makes the Beringian route the only significant contender during the Tertiary and requires climatic optima for SDD to move *Crataegus* through Beringia. But the frequency of this is considered relatively low on paleoclimatic grounds and the small number of similar *Crataegus* phylads on both sides of the Pacific. Fossil evidence, although requiring modern updating, suggests plentiful *Crataegus* in North America from the Mid-Tertiary. The origin of the genus is hard to time at present but late Eocene can stand as the midpoint of several possibilities.

One is thus left with two broad evolutionary options, specifically, '*Americanae*' being derived from '*Sanguineae*' (Fig. 32), the most likely solution, in spite of certain difficulties with it, or parallel development in both macro-continents from *scabrifolioid* and *mexicanoid* stock after only one successful Beringian event (Fig. 33). The procladogram currently favors this, but only on gradistic grounds. This may well be changed by further evidence (and is challenged by known Alaskan migration potential). Not enough is known about some peculiar species, which may be intermediates between existing taxa, or relicts of older radiation. But not one of these bears on the choice between the two models presented above. A collapsing of the time-scale, which may prove necessary, as evidence accumulates, should not of itself affect the form of the cladogram.

Thus, *Crataegus* has changed, due to modern researches, from a genus in which taxonomy and cladistics had appeared overwhelmingly difficult, to, in some senses, the very opposite—a para-

digm of an SDD genus with long life history, evolving mainly during the Tertiary, and evidencing both evolutionary bursts, probable periods of phenetic gradualism, and, if our feelings about the proposed relicts are correct, almost total stasis in some cases. Overwhelming evidence from phenetics, modern biogeography, reproductive biology, dispersal biology, paleogeography, paleoclimate, fossils, and outgroup analysis, generates a model of *Crataegus* evolution that is the clearest to date, and, in fact, totally novel.

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APPENDIX A. PROVISIONAL CHECKLIST OF WORLD *CRATAEGUS*

Arranged by section and series. ? = assignment to this section or series uncertain. Subscripted numbers, e.g. "62a. *C. glabriuscula* Sarg." = not certainly different from others with same number (e.g. 62, 62b, etc.). Sources: regional floras cited in text except for Mexico (Harvard University Herbaria), supplemented by a variety of local floras.

† = sample used in biogeographic analysis.

* = sample used in taxonomic studies.

Sect. Mexicanae Loud.

Ser. Mexicanae (Loud.) Rehd.

†*1. *C. mexicana* Moc. & Sessé

Ser. 'Henryanae (Sarg.)'

†*2. *C. scabrifolia* (Franch.) Rehd.

Sect. Oxyacanthae Loud.

Ser. Oxyacanthae (Loud.) Rehd.

†*3. *C. monogyna* Jacq.
*4. *C. curvisepala* Lindm. (= *C. calycina* auct. non Peterm.)
5. *C. macrocarpa* Hegetschw.
*6. *C. kyrtostyla* Fingerh.
7. *C. turkestanica* Pojark.
8. *C. pseudoheterophylla* Pojark.
*9. *C. laevigata* (Poir.) DC.
10. *C. turcomanica* Pojark.
11. *C. ambigua* C. A. Mey. ex Beck.
12. *C. volgensis* Pojark.
13. *C. transcaspica* Pojark.
14. *C. persica* Pojark.
15. *C. caucasica* C. Koch
*16. *C. atrosanguinea* Pojark.
*17. *C. songarica* C. Koch
18. *C. sphaenophylla* Pojark.
*19. *C. microphylla* C. Koch
20. *C. stevenii* Pojark.
21. *C. beckeriana* Pojark. (= *C. pallasii* Griseb. in Fl. Eur.)
22. *C. ucrainica* Pojark.
*23. *C. meyeri* Pojark. }
24. *C. eriantha* Pojark. } series Erianthae Pojark. ? → Azaroli
25. *C. taurica* Pojark. }

(+ putative hybrids: *C. palmstruchii* Lindm., *C. leiomonogyna* Lkok., *C. heterodonta* Pojark., *C. poloniensis* Cin., *C. subborealis* Cin., *C. allemaniensis* Cin., *C. orientobaltica* Cin., *C. insularis* Cin.)

Ser. Apiifoliae (Loud.) Rehd.

†*26. *C. marshallii* Egglest.

Ser. Pentagynae (Schneid.) Rus.

*27. *C. pentagyna* Waldst. & Kit.
28. *C. davisii* Browicz (close to *C. pentagyna*—Fl. Turkey)
29. *C. pseudomelanocarpa* M. Pop. (eastern counterpart to *C. pentagyna*—Pojarkova)

Ser. Azaroli (Loud.) Rehd.

30. *C. pycnoloba* Boiss. & Heldr.
*31. *C. orientalis* Pall.
32. *C. laciniata* Ucria
*33. *C. tanacetifolia* (Lam.) Pers.
*34. *C. azarolus* L. (incl. *C. aronia* (L.) Bosc.)
*35. *C. pontica* C. Koch
36. *C. szovitsii* Pojark.
37. *C. sinaica* Boiss.
38. *C. dikmensis* Pojark.
*39. *C. heildreichii* Boiss.

Sect. Sanguineae Zabel ex Schneid.

Ser. Pinnatifidae (Zabel ex Schneid.) Rehd.

†*40. *C. pinnatifida* Bunge

Ser. Nigrae (Loud.) Rus.

*41. *C. nigra* Waldst. & Kit.
42. Original is deleted from list.
*43. *C. jozana* C. K. Schneid.

Ser. Sanguineae (Zabel ex Schneid.) Rehd.

†*44. *C. sanguinea* Pall. ex Bieb.
†*45. *C. dahurica* Koehne ex C. K. Schneid.
†*46. *C. altaica* Lange
47. *C. wattiana* Hemsl. ex Lace (? = *C. korolkowii* Henry)

Ser. (un-named)
- †*48. *C. maximowiczii* C. K. Schneid.
- †49. *C. chlorosarca* Maxim.
- †*50. *C. kansuensis* Wils.
- †51. *C. chungtiensis* W. W. Smith
- 52. *C. aurantia* Pojark.
- 53. *C. remotilobata* H. Raik. ex Pop.

Ser. (un-named)
- *54. *C. clarkei* Hook. f.
- †*55. *C. wilsonii* Sarg.
- †56. *C. oresbia* W. W. Smith

Sect. (un-named)
- †*57. *C. hupehensis* Sarg.
- †58. *C. shensiensis* Pojark.

Sect. Cuneatae Rehd. ex Schneid.
- †*59. *C. cuneata* Sieb. & Zucc.
- *60. *C. tangchungchangii* Metcalf (?)

Sect. Cordatae Beadle ex Egglest.
- †*61. *C. phaenopyrum* (L. f.) Medic.

Sect. Virides Sarg. ex Schneid.

Ser. Virides (Sarg. ex Schneid.) Rehd.
- †*62. *C. viridis* L.
- 62a. *C. glabriuscula* Sarg.
- 62b. *C. sutherlandensis* Sarg.
- 62c. *C. anamesa* Sarg.
- 62d. *C. stenosepala* Sarg.
- 62e. *C. poliophylla* Sarg.
- †*63. *C. nitida* (Engelm.) Sarg.

Ser. Pulcherrimae (Sarg. ex Palmer) Palmer
- 64. *C. pulcherrima* Ashe

Sect. Microcarpae Loud.
- †*65. *C. spathulata* Michx.

Sect. Flavae Loud.
- †*66. *C. flava* Ait.
- 67. *C. aprica* Beadle
- 68. *C. michauxii* Pers.
- 69. *C. floridana* Sarg.
- 70. *C. lacrimata* Small

Sect. Parvifoliae Loud.
- †*71. *C. uniflora* Muenchh.

†Sect. Aestivales Sarg. ex Schneid.
- *72. *C. aestivalis* (Walt.) T. & G.
- 73. *C. opaca* Hook. & Arn.
- 74. *C. rufula* Sarg.
- 75. *C. maloides* Sarg. (incl. *C. fruticosa* Sarg., *C. luculenta* Sarg.)

Sect. Brevispinae Beadle ex Schneid.
- †*76. *C. brachyacantha* Engelm. & Sarg.

Sect. Douglasii Loud.
- †*77. *C. douglasii* Lindl.
- †*78. *C. rivularis* Nutt.
- 79. *C. erythropoda* Ashe (incl. *C. cerronis* Nels.)
- †80. *C. saligna* Greene (? correctly placed)

Sect. Crus-galli Loud.

Ser. Crus-galli (Loud.) Rehd.
- †*81. *C. crus-galli* L., sens. lat. (incl. *C. fontanesiana* Spach, *C. bushii* Sarg., *C. livoniana* Sarg., *C. pyracanthifolia* Beadle, etc., etc.)
- 81a. *C. reverchonii* Sarg.
- 81b. *C. cherokeensis* Sarg.
- 81c. *C. sublobulata* Sarg.
- 81d. *C. engelmannii* Sarg.
- †81e. *C. tracyi* Ashe
- 82. *C. berberifolia* T. & G.
- †83. *C. baroussana* Egglest. (?)
- †84. *C. parryana* Egglest. (?)

Ser. Punctatae (Loud.) Rehd.
- *††85. *C. punctata* Jacq.
- †85a. *C. collina* Chapm.
- †86. *C. brazoria* Sarg. (?)
- 87. *C. disperma* Ashe

Sect. Triflorae Beadle ex Schneid.
- †*88. *C. triflora* Chapm.
- 89. *C. austromontana* Beadle
- 90. *C. conjungens* Sarg.

Sect. 'Americanae (El-Gazaar)'

†Ser. Bracteatae (Palmer) Rehd.
- 91. *C. ashei* Beadle
- *92. *C. harbisonii* Beadle
- 93. *C. pearsonii* Ashe (?)

Ser. (un-named)
- †94. *C. viburnifolia* Sarg.

Ser. Molles (Sarg. ex Schneid.) Rehd.
- †*95. *C. mollis* (T. & G.) Scheele
- †95a. *C. noelensis* Sarg.
- 95b. *C. viburnifolia* Sarg.
- †95c. *C. texana* Buchel.
- †95d. *C. limaria* Sarg.
- 96. *C. canadensis* Sarg.
- 96a. *C. arnoldiana* Sarg.
- 96b. *C. anomala* Sarg.
- 97. *C. pensylvanica* Ashe
- †98. *C. greggiana* Egglest.
- †*99. *C. submollis* Sarg.

†*Ser. Coccineae (Loud.) Rehd.
- *100. *C. holmesiana* Ashe
- *101. *C. pedicellata* Sarg.
- *102. *C. pringlei* Sarg.
- 103. *C. acutiserrata* Kruschke
- 104. *C. fulleriana* Sarg.
- *105. *C. corusca* Sarg.

Ser. Tenuifoliae (Sarg. ex Egglest.) Rehd.
- †**106. *C. macrosperma* Ashe
- 107. *C. apiomorpha* Sarg.
- *108. *C. fluviatilis* Sarg.
- †*109. *C. schuettei* Ashe
- *110. *C. lucorum* Sarg.
- †*111. *C. flabellata* (Bosc.) K. Koch

Ser. Rotundifoliae (Egglest. ex Egglest.) Rehd.
- †112. *C. columbiana* Howell
- †*113. *C. chrysocarpa* Ashe
- †*114. *C. dodgei* Ashe
- *115. *C. flavida* Sarg.
- †116. *C. margaretta* Ashe
- 117. *C. irrasa* Sarg.
- 118. *C. aboriginum* Sarg.
- 119. *C. laurentiana* Sarg.

†Ser. Intricatae (Sarg. ex Schneid.) Rehd.
- *120. *C. intricata* Lange
- 121. *C. foetida* Ashe

Ser. Brainerdianae Palmer
†*122. *C. brainerdii* Sarg.
123. *C. sylvestris* Sarg.
†*124. *C. scabrida* Sarg.
125. *C. coleae* Sarg.
*126. *C. jonesae* Sarg. (?)

Ser. Macracanthae (Loud.) Rehd.
*127. *C. succulenta* Link
†*128. *C. macracantha* Lodd.
†*129. *C. calpodendron* (Ehrh.) Medic.

†Ser. Silvicolae (Palmer) Kruschke
*130. *C. iracunda* Beadle
*131. *C. compacta* Sarg.
*132. *C. suborbiculata* Sarg.
133. *C. nitidula* Sarg.
134. *C. compta* Sarg.
135. *C. prona* Sarg.
136. *C. opulens* Sarg.
137. *C. jesupii* Sarg.
138. *C. beata* Sarg.
139. *C. incerta* Sarg.
(? others)

Ser. Pruinosae (Sarg. ex Egglest.) Rehd.
†***140. *C. pruinosa* (Wendl.) K. Koch, sens. lat.
141. *C. formosa* Sarg.
*142. *C. dissona* Sarg.

†Ser. Dilatatae (Sarg. ex Palmer) Rehd.
*143. *C. dilatata* Sarg. (= *C. conspecta* Sarg.)
144. *C. coccinioides* Ashe
145. *C. glareosa* Ashe (?)

THE DISTRIBUTION OF SCROPHULARIACEAE IN THE HOLARCTIC WITH SPECIAL REFERENCE TO THE FLORISTIC RELATIONSHIPS BETWEEN EASTERN ASIA AND EASTERN NORTH AMERICA[1]

HONG DE-YUAN[2]

ABSTRACT

Based on a general survey of the distribution of Scrophulariaceae in the Holarctic, eastern Asia is shown to be the richest in members of the family among five regions. Western North America has 53% of the genera (16/30) common to eastern Asia, whereas eastern North America has 48% of the genera (17/35) common to eastern Asia. Among 14 genera (excluding the cosmopolitan and pantropical genera) shared by North America and Eurasia, four distributional patterns are recognized: temperate western North America/Mediterranean disjunction (one genus); temperate Eurasia/North America disjunction (three genera); temperate eastern Asia/eastern North America disjunction (four genera), and continuous distribution through the Bering Strait or Aleutian Islands (six genera). Three phases of plant communication between North America and Eurasia are hypothesized. The origin and migration routes of some taxa are traced. Six genera are suggested to have migrated from eastern Asia to North America and four genera are considered to have migrated in the opposite direction, i.e., from western North America to eastern Asia through Beringia or the Bering Strait.

The floristic affinity between eastern Asia and eastern North America was first noticed by Linnaeus (in a dissertation defended by J. Halenius; see Graham, 1972) as early as 1750 and has been the focus of much attention by plant geographers since Gray's (1840, 1846; reprinted in Graham, 1972) brilliant works. The subject has been extensively discussed over the past century (see Li, 1952; Graham, 1972, for literature). There have been, however, few, if any, discussions on the subject pertaining to individual families, probably due in part to a lack of floristic work on China, the major part of eastern Asia, in the past. This report is intended to be an initial effort in this direction.

The area covered in this work is the Holarctic Kingdom (Takhtajan, 1969) or Melchior's (1964) Kingdom I. To facilitate an analysis of distribution and discussion, the kingdom is divided into five regions, i.e., eastern North America (east of the Rocky Mountains, corresponding basically to Takhtajan's region 4), western North America (Takhtajan's regions 5 plus 9), eastern Asia (Takhtajan's region 3 plus the eastern half of region 2, or Good's (1974) regions 3 plus 2B), western and central Asia (Takhtajan's region 8 or Irano-Turanian Region), and Europe and the Mediterranean together (including the Azores).

GENERAL ASPECT

The Scrophulariaceae are a rather large family, containing 18 tribes, about 200 genera, and 3,000 species. It is highly developed in the Holarctic Kingdom with 14 tribes, 110 genera, and over 2,200 species. The tribes Verbasceae, Paulownieae, Hemiphragmeae, Ellisiophylleae (if included in the family), and Collinsieae are endemic to the area, and the Antirrhineae, Veroniceae, Rhinantheae, and Digitaleae have most of their members here. Of the 110 genera, 72 are endemic. The family, however, also flourishes in the Southern Hemisphere, with the tribes Aptosimeae, Calceolarieae, Hemimerideae, Manuleae, and Aragoeae (Hong & Nilsson, unpubl.) entirely or mainly confined there.

Table 1 shows that of the five regions mentioned above, eastern Asia has the most tribes, the most genera, the most endemic genera, the most species, and the most endemic species. It is the only subregion with endemic tribes (3). The least number of genera occur in western North America and the fewest species (including endemic ones) in eastern North America. North America, as a whole, is comparatively poor in scrophulariaceous plants, having only nine tribes (one endemic), 48 genera (16 endemic), and ca. 630 species (ca. 600 endemic).

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TABLE 1. Taxa in the five regions in North America and Eurasia.

	Number of Taxa in Eurasia				Number of Taxa in North America		
Taxon	E. Asia	W. & C. Asia	Europe & Medit.	Total	E. North America	W. North America	Total
Tribe	11 (3)	8 (0)	8 (0)	12 (4)	8 (0)	8 (0)	9 (1)
Genus	58 (22)	35 (5)	39 (7)	82 (43)	35 (8)	30 (6)	48 (16)
Species	700 (550)	600 (350)	650 (450)	1,750 (1,650)	160 (100)	500 (450)	630 (600)

Western North America/eastern Asia have 16 genera in common; and eastern North America/eastern Asia have 17 genera in common. These paired regions share a greater number of taxa than any of the other paired regions. Thus, in the number of genera shared, the two regions in North America are both closer to eastern Asia than to Europe and Mediterranean together and to western and central Asia. All the large genera in North America have the great majority of their members in the western part of the continent, with few species (*Penstemon, Castilleja,* and *Mimulus*) or only a single species (*Orthocarpus*) extending into the eastern part. It is of interest to note that all four of these genera also occur in eastern Asia. Furthermore, 53% of the genera in western North America are in eastern Asia, whereas 48% of the genera in eastern North America are common to eastern Asia. It is probably reasonable to say that the relationships of the Scrophulariaceae between western North America and eastern Asia are closer than those between eastern North America and eastern Asia.

The Distributional Patterns of the Taxa Shared by North America and Eurasia

North America and Eurasia share six tribes (Anthirrhineae, Gerardieae, Gratioleae, Rhinantheae, Scrophularieae, and Veroniceae) and 19 genera (*Antirrhinum, Bacopa, Buchnera, Castilleja, Euphrasia, Gratiola, Lagotis, Limosella, Linaria, Linderia, Melampyrum, Mimulus, Orthocarpus, Pedicularis, Penstemon, Rhinanthus, Scrophularia, Veronica,* and *Veronicastrum*) disjunctly distributed across the Atlantic and/or the Pacific. Since the genera *Bacopa, Gratiola, Limosella, Linderia* (all members of the tribe Gratioleae) and *Buchnera* (Buchnereae) are either cosmopolitan aquatics or pantropical, it is better to omit them for the analysis. The genus *Mimulus,* a widely distributed member of the tribe Gratioleae, is considered because it is best represented in the kingdom, particularly in western North America and shows a special relationship between western North America and eastern Asia.

Different taxonomic ranks are involved in these disjunct distributions. At the tribal level, a number of paired genera are found disjunctly distributed, one member of each pair in North America and the counterpart in Eurasia. In the tribe Veroniceae, *Veronica* on one side and *Synthyris* and *Besseya* together on the other are such a case. *Veronica* is a large and polymorphic genus, with its center from the Pyrenees, along the Alps, north Anatolia, the Caucasus, the Himalayas, and the Pamirs to southwest China and Tienshan, where all eight sections and the majority of species exist. Only a few species (excluding cosmopolitan and weedy ones) mostly belonging to the section *Veronica,* extend into tropical Africa, Australia, and North America. *Synthyris* and *Besseya* together may be its counterpart in North America (Fig. 1). The relationships between *Veronica* and the other two genera are so close that no differences, except for habit and chromosome number, are useful for distinguishing them. *Siphonostegia, Lesquereuxia,* and *Schwalbea* in Rhinantheae provide another example. The first occurs in eastern Asia, the second in Greece and southern Turkey, and the third in eastern North America (Fig. 2). *Siphonostegia* differs from the other two in having pinnatifid leaves and subequal calyx lobes; *Lesquereuxia* is different from *Schwalbea* mainly in its opposite leaves. The three are closely related (Hedge, 1978).

The 14 genera common to the two continents may be grouped into four categories according to their distributional patterns:

1) Disjuncts across the Atlantic (with one part of the area in Europe and the Mediterranean region and the other in North America). Only one genus, *Anthirrhinum,* falls into this category. It consists of 30 species, 17 of them occurring in the western Mediterranean west of Italy; the oth-

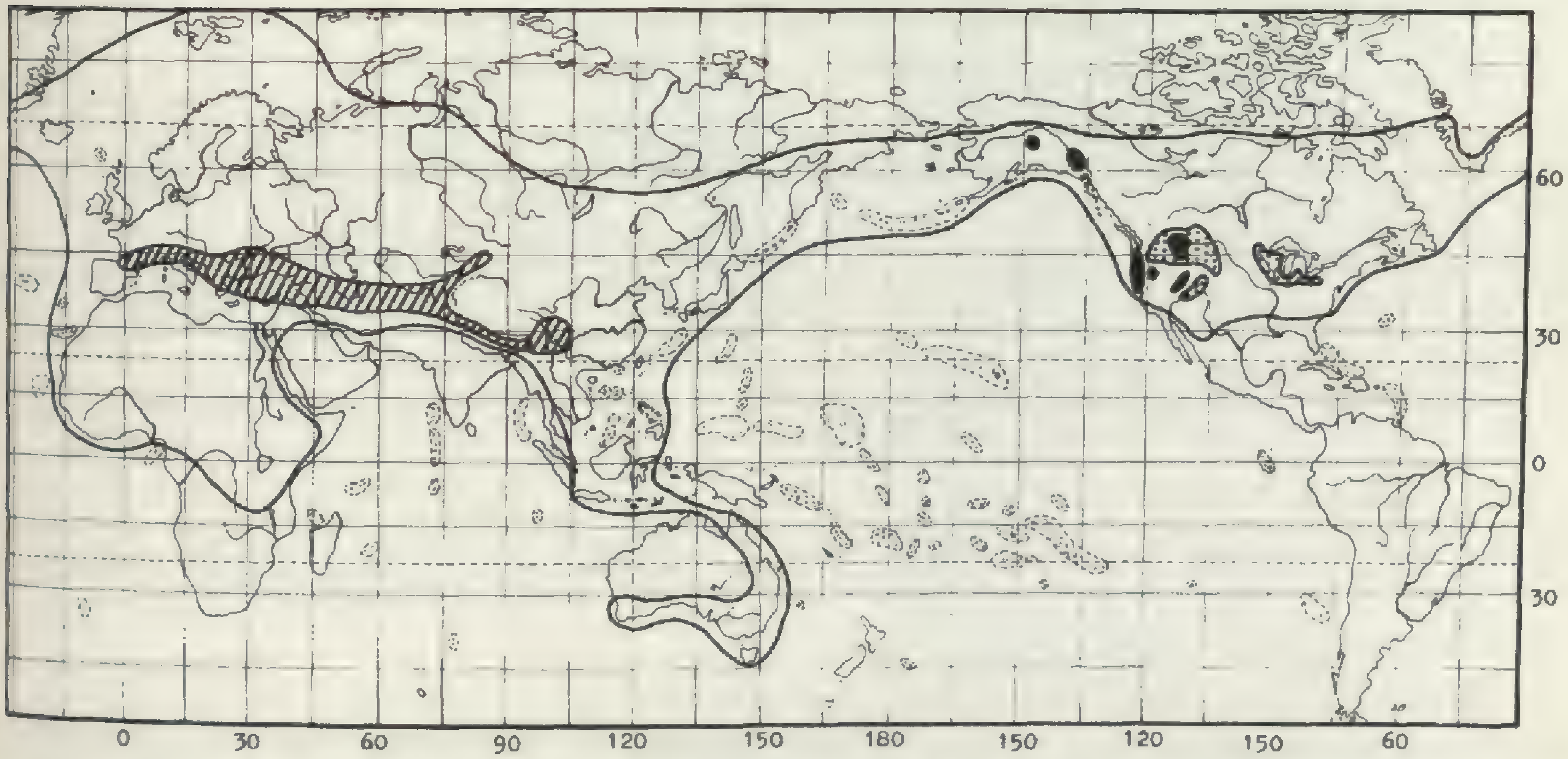

FIGURE 1. Distribution of the genera *Veronica, Synthyris,* and *Besseya.* Although *Veronica* is distributed almost worldwide, the majority of species and all eight sections occur in the southern Holarctic Kingdom (the cosmopolitans are not included in the map). *Synthyris* is totally in western North America and *Besseya* has only one species in eastern North America. *Synthyris* and *Besseya* may be regarded as congeneric. Shaded area—distribution center of *Veronica*; black area—*Synthyris*; dotted area—*Besseya.*

er 13 are restricted to California in the United States (Fig. 3).

2) Genera disjunct across both the Pacific and the Atlantic (that is with one part of the area in temperate Eurasia and the other in temperate North America). In this category are three genera, *Scrophularia, Linaria,* and *Melampyrum,* all centered mainly in southern Europe and the Mediterranean. *Scrophularia* is a large genus with ca. 150 species, of which over 100 grow in the region from the Pyrenees to the Pamirs, and with ca. 20 in a small area in southwest China (Fig. 4). In North America the genus has nine species (or only two species depending on species concept). The situation in *Linaria* appears similar (Fig. 5). It is centered in the Mediterranean re-

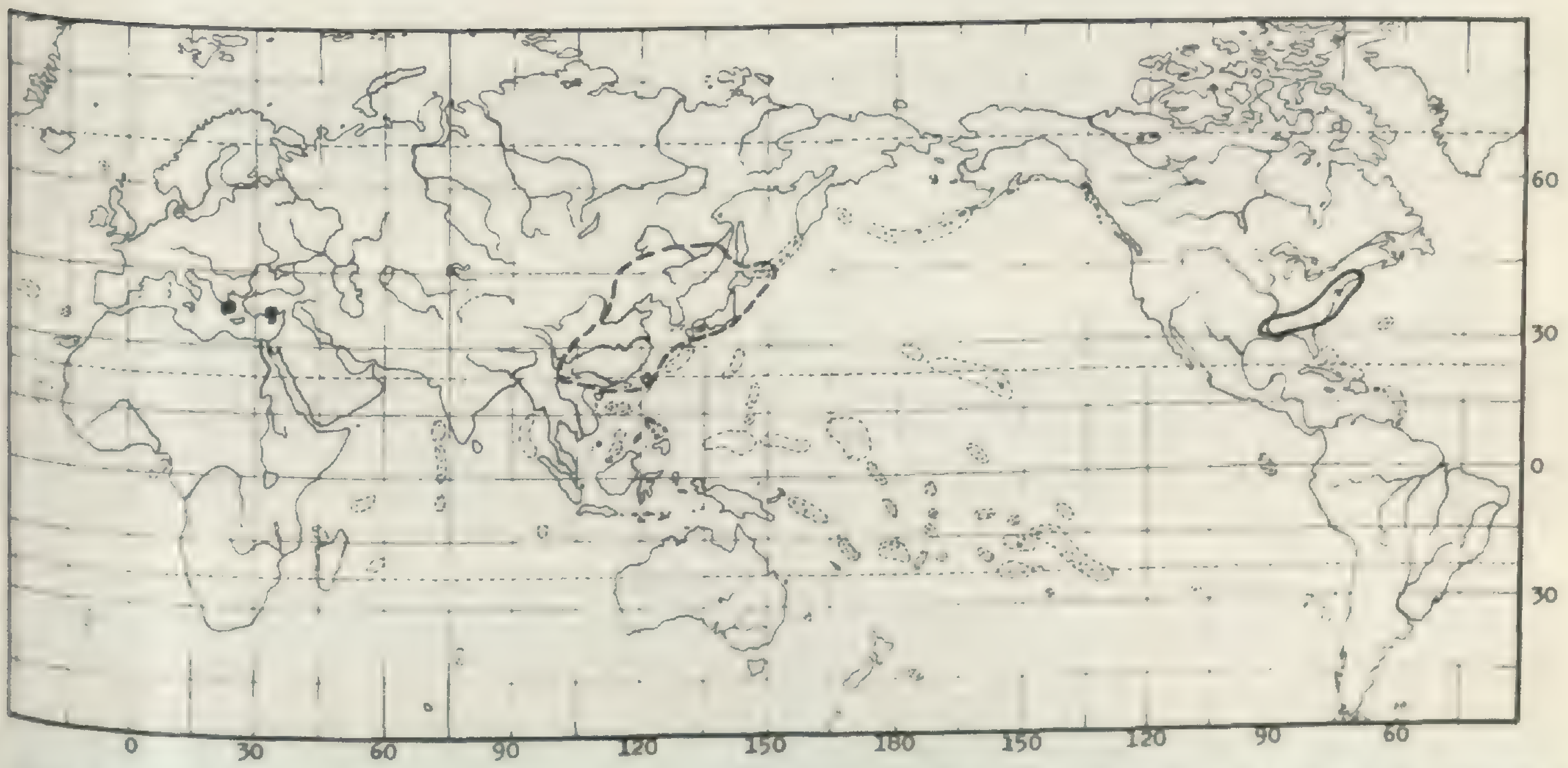

FIGURE 2. Distribution of three very closely related genera, *Schwalbea* (continuous line), *Siphonostegia* (broken line), and *Lesquereuxia* (two black dots).

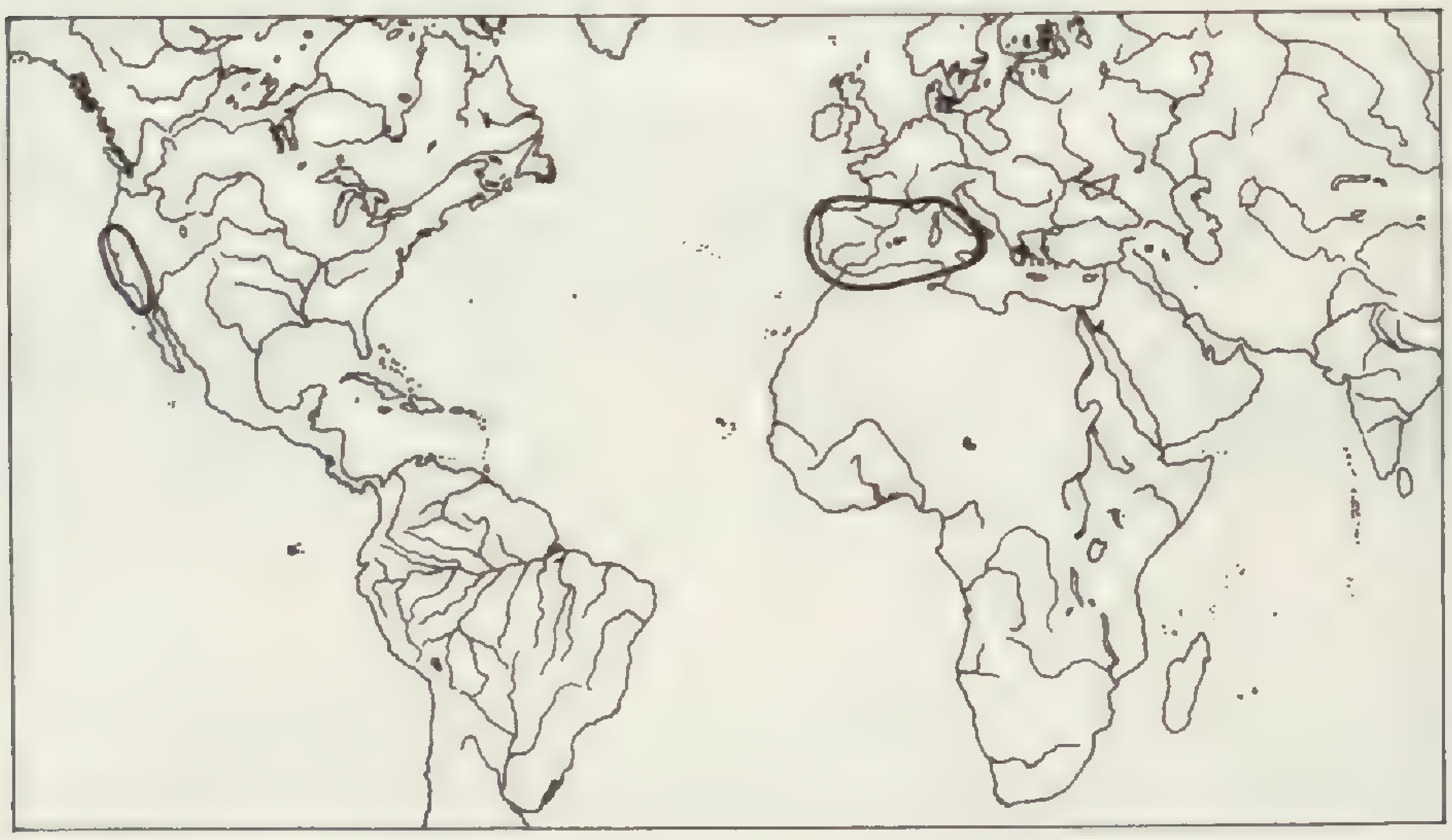

Figure 3. Disjunct distribution of *Antirrhinum.*

gion (where more than 80 of ca. 120 species occur), particularly in Portugal and Spain. Only one or two species grow in North America. *Melampyrum* is a much smaller genus with ca. 30 species, two-thirds of which are concentrated in southeast Europe and the Caucasus. Only one polymorphic species, *M. lineare,* occurs in temperate North America (Fig. 6).

3) Genera disjunct across the Pacific (with one part in North America and the other in east Asia). Four genera (*Penstemon, Mimulus, Veronicastrum,* and *Orthocarpus*) belong to this category. All but *Veronicastrum* have the majority of their members in western North America. *Penstemon* consists of some 220 species, with a great majority concentrated in temperate western North America, but with one species, *P. frutescens,* in Kamchatka, the Kuriles, northern Japan, and Sakhalin (Fig. 7). *Orthocarpus* occurs almost entirely in western North America. Only one species extends eastward into the eastern part of the continent; another isolated species grows in Andean America. A new species, *O. chinensis,* was recently discovered from central China (Hong, 1979). Thus, *Orthocarpus* is actually disjunct between western North America and eastern Asia (Fig. 8). Although the genus *Mimulus* is widely distributed, abundance and center of diversity is again in western North America where over two-thirds of the total number of species (ca. 70/110) grow; the Asian part of the range is a strip from the south Kuriles and Sakhalin to the Himalayas and is distantly disjunct from the Australian and African parts of the range of the genus (Fig. 9).

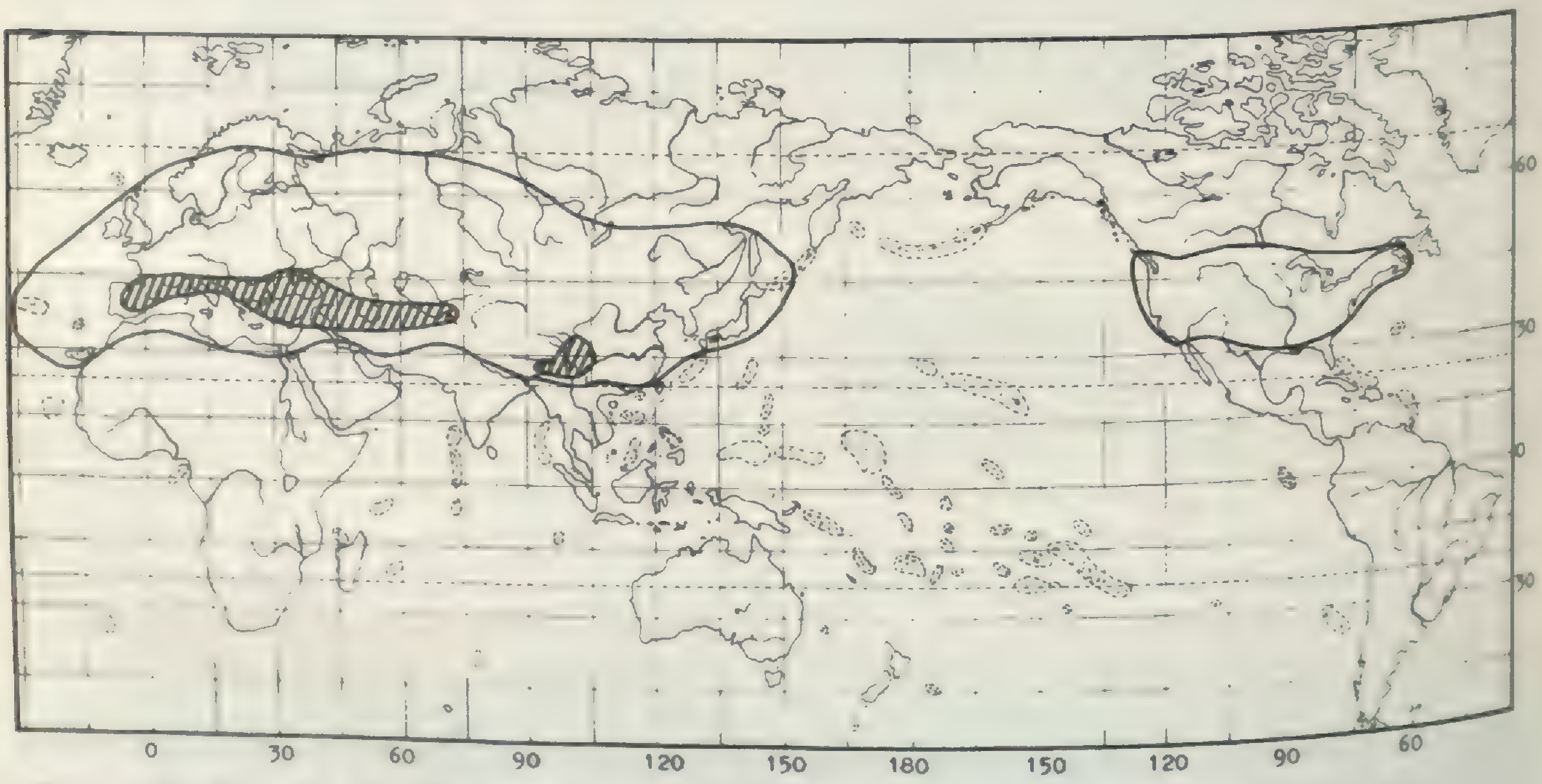

Figure 4. Disjunct distribution of *Scrophularia.* The distribution center is shaded.

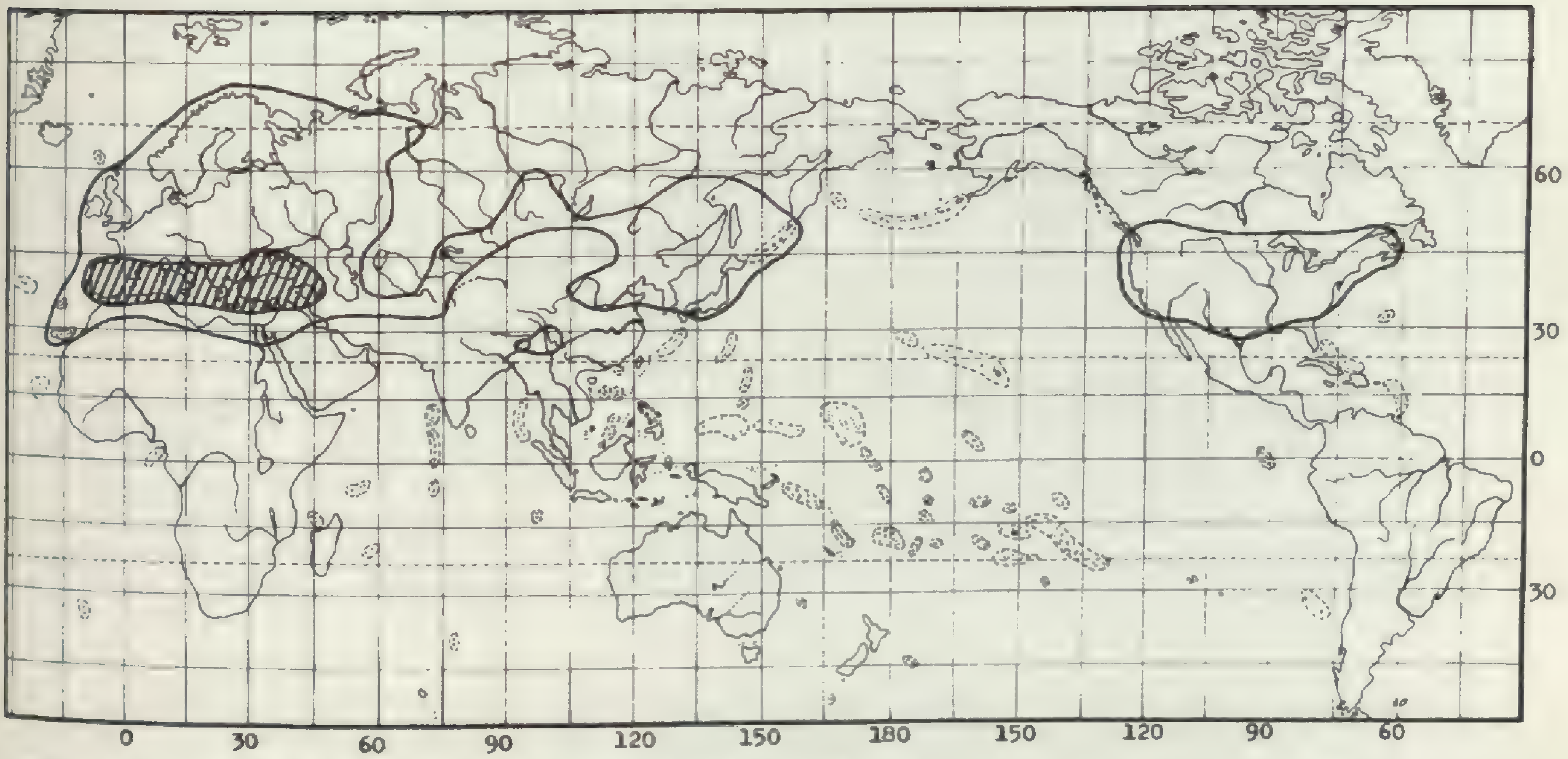

FIGURE 5. Disjunct distribution of *Linaria*. The shaded area indicates the distribution center.

The discontinuous distribution of *Veronicastrum* was noted by Li (1952) in his discussion of floristic relationships between eastern Asia and eastern North America. The genus has 19 species in eastern Asia, from the eastern Himalayas to Sakhalin, and a single species in eastern North America south of 50°N (Fig. 10).

4) Genera continuously distributed across the northern Pacific. In this category are six genera, *Veronica, Lagotis, Pedicularis, Euphrasia, Rhinanthus,* and *Castilleja.* As mentioned above, *Veronica* is a large genus with the majority of its species in temperate Eurasia, but with 13 species native to North America (excluding the cosmopolitan species). Seven are endemic, three (*V. alpina, V. fruticans,* and *V. scutellata*) are circumpolar, and *V. stelleri* occurs from the Chang-Bai Mountain in northeast China to southern Alaska across the Aleutians (Fig. 11). *Lagotis* is mainly an eastern Asian genus centered in southwestern China; only two species extend into northeastern Europe and one into the Caucasus. *Lagotis glauca,* however, reaches Alaska and the Yukon in the northwestern corner of Canada (Fig. 12). *Pedicularis,* the largest genus in the Scrophulariaceae, with ca. 500 species, is typical of the

FIGURE 6. Disjunct distribution of *Melampyrum*. The distribution center is indicated by the shaded area.

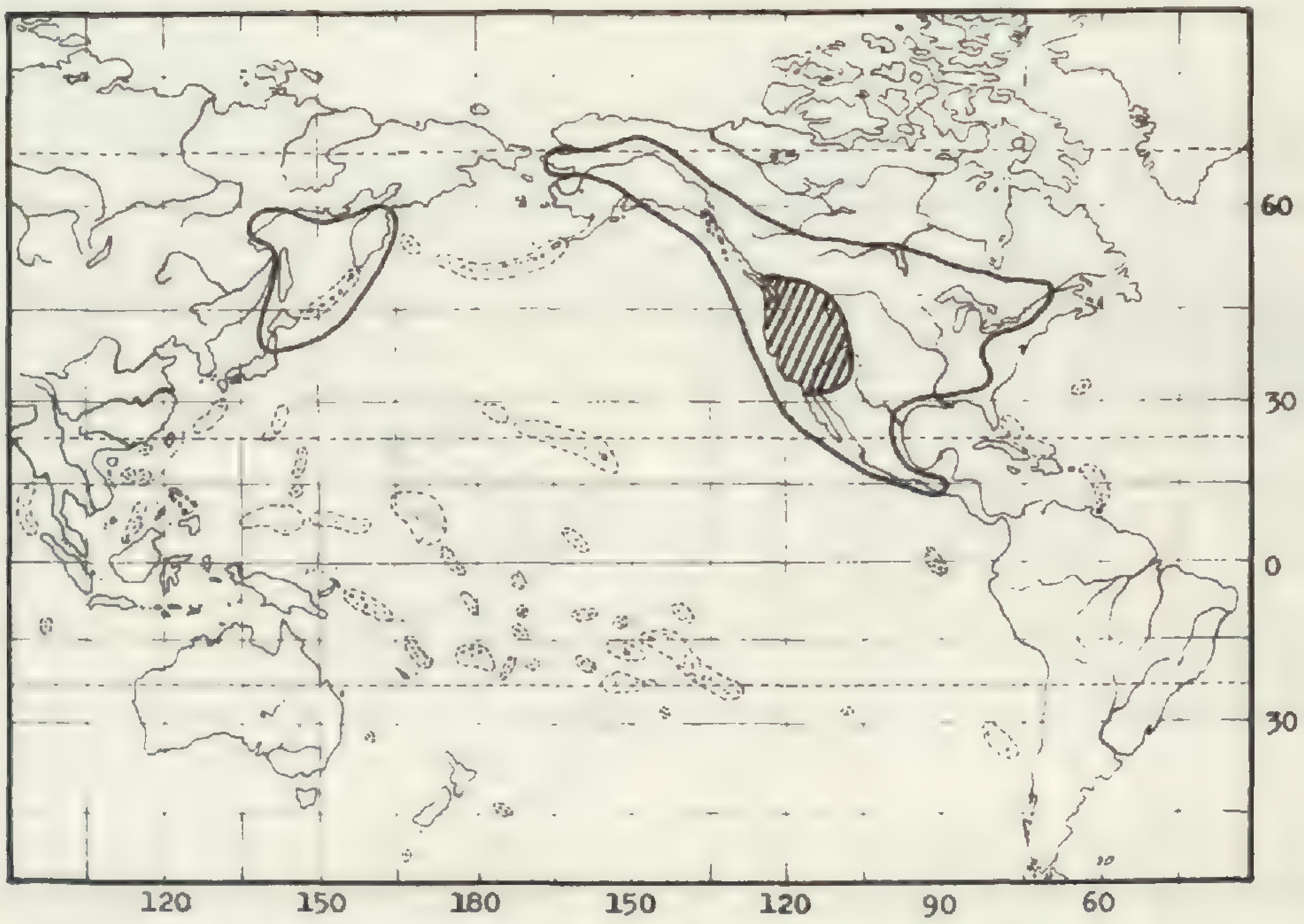

FIGURE 7. Disjunct distribution of *Penstemon*. Shaded area indicates distribution center. Only one species, *P. frutescens*, occurs in eastern Asia.

Holarctic Kingdom. Over 300 species are concentrated in a small area in the eastern Himalayas, western Sichuan, and northwestern Yunnan. Among the 32 species native to North America, 12 are common to eastern Asia and eight are common to Europe (Fig. 13). Although *Euphrasia* is widespread, section *Euphrasia*, consisting of annuals, is totally within the Holarctic Kingdom with the greatest number of species in Europe. Native to North America are seven species, four endemic to the eastern part; two are also in northern Europe and one is also in eastern Asia (Fig. 14). *Rhinanthus* is to some extent similar to *Euphrasia* section *Euphrasia*, but there are two gaps in the continental part of the range in the Far East and Kamchatka and only a single species, *R. borealis*, occurs in North America (Fig. 15). *Castilleja* is different from the genera mentioned above in that it extends to South America and is centered in western North

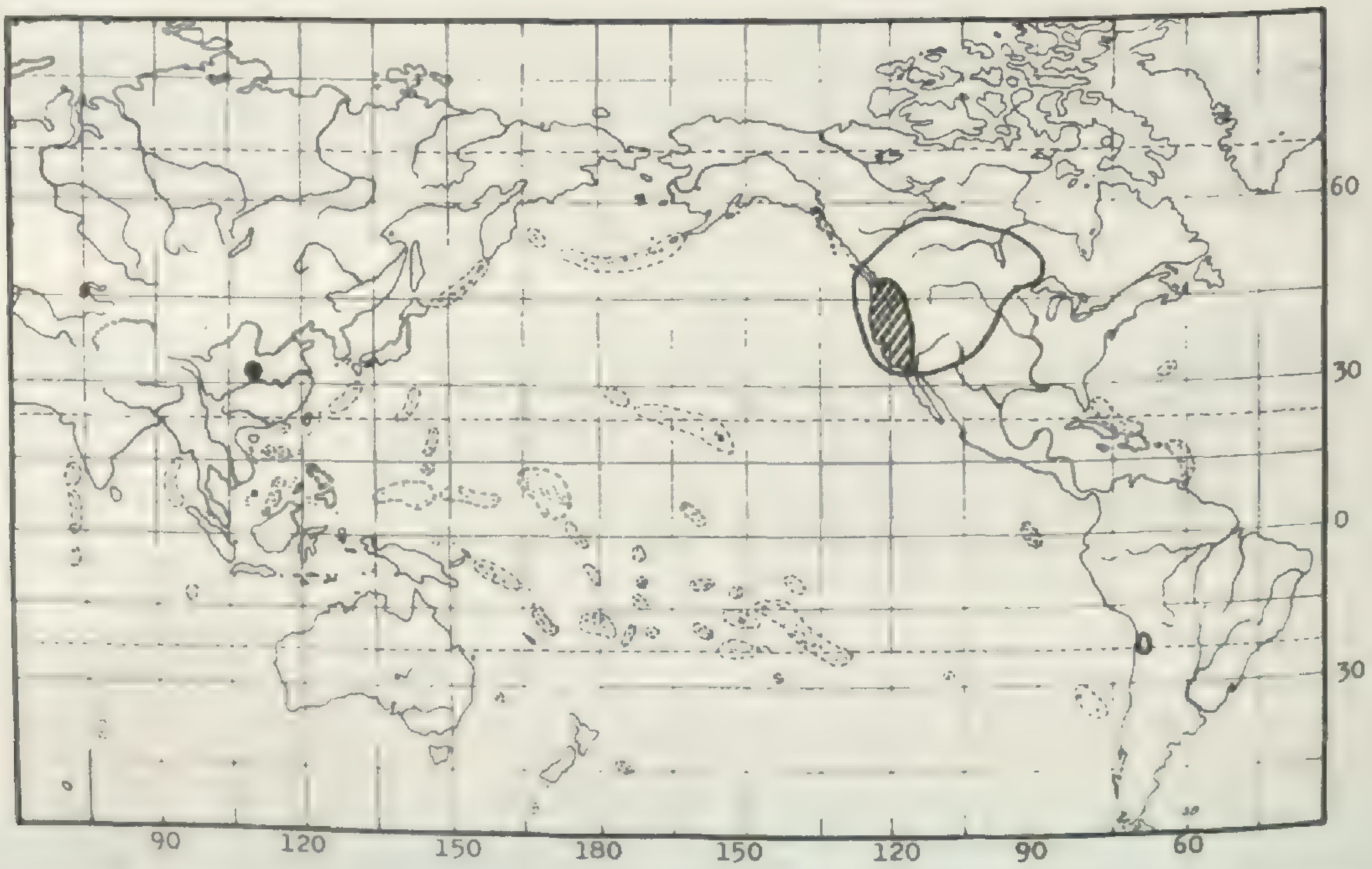

FIGURE 8. Disjunct distribution of *Orthocarpus*. The distribution center is indicated by the shaded area. Black dot—one single Asian species, *O. chinensis* Hong.

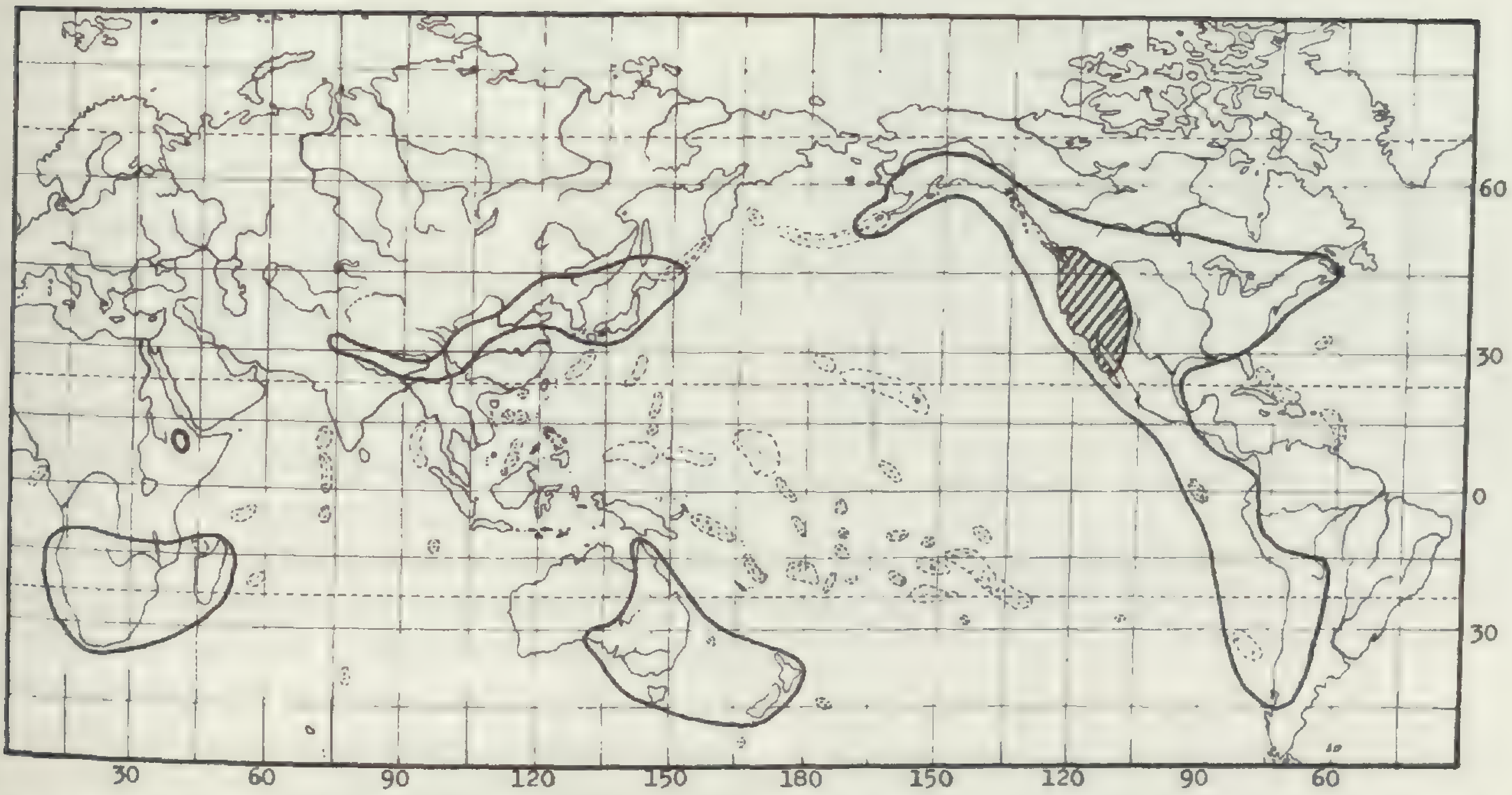

FIGURE 9. Distribution of *Mimulus.* The distribution center is indicated by the shaded area. All the Asian species but *M. strictus,* which is conspecific with the African plants, belong to the section *Paradanthus,* also centered in the Pacific Coast states.

America, with only three species in northern Eurasia (Fig. 16).

In summary, in the Holarctic Kingdom the Scrophulariaceae have six tribes disjunctly distributed in Eurasia/North America. Four of them, the Antirrhineae, Rhinantheae, Scrophularieae, and Veroniceae, are typically or mostly northern tribes. The Antirrhineae are mainly in the Mediterranean region where there are eight genera (including three endemic or nearly endemic ones); the Rhinantheae is best developed in eastern Asia where there are 14 genera (seven endemic); the Scrophularieae is almost equally developed in Eurasia and North America; the Veroniceae have 13 genera in Eurasia, particularly in the southern part, and four genera in North America. Between North America and Eurasia there is also a genus-pair distributional pattern, *Schwalbea/Siphonostegia-Lesquereuxia.* Among 14 northern genera common to North America and Eurasia (five additional pantropical or worldwide genera are out of our consideration) one falls into a Mediter-

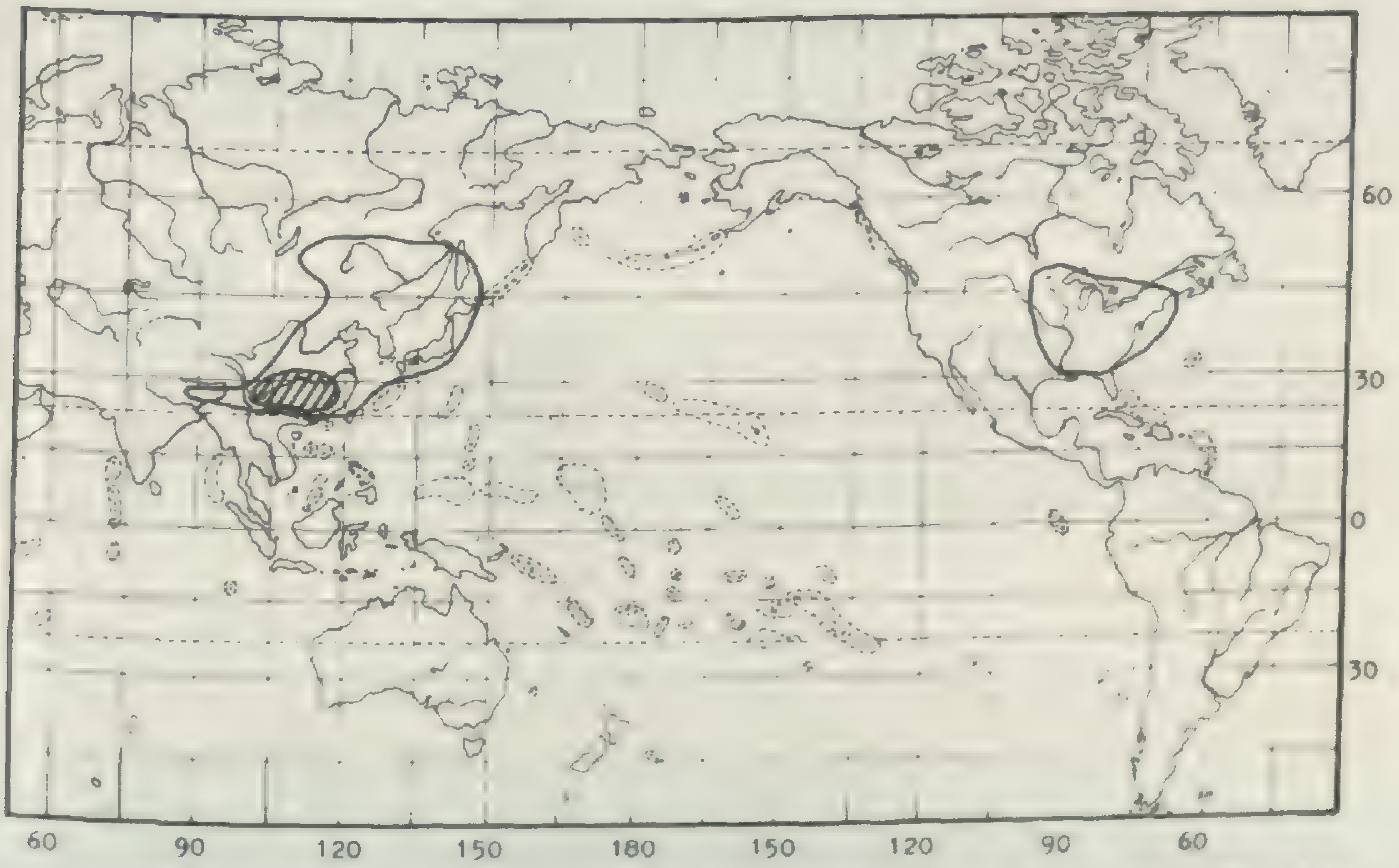

FIGURE 10. Disjunct distribution of *Veronicastrum.* Shaded area indicates the distribution center.

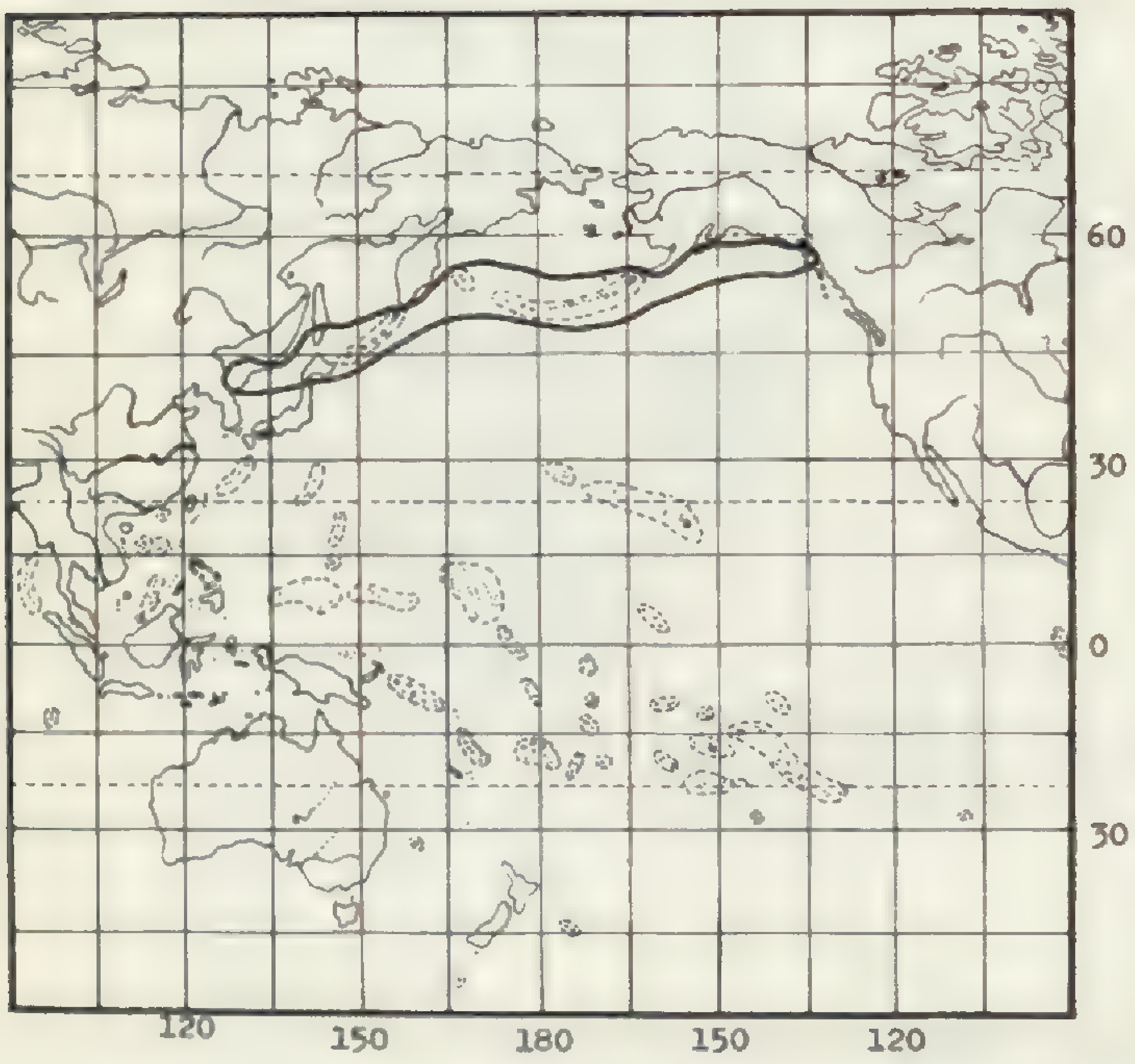

FIGURE 11. Distribution of *Veronica stelleri.*

ranean/western North America pattern; three into a temperate Eurasia/North America pattern; four into a temperate eastern Asia/North America pattern (three are of an eastern Asia/western North America pattern; one is of an eastern Asia/eastern North America pattern). The remaining six are more or less continuously distributed, with small gaps in the Bering Strait or Aleutian regions. One of these is primarily an American genus; five are Eurasian ones (three with eastern Asia as their distributional center).

THE PHASES OF PLANT COMMUNICATION BETWEEN NORTH AMERICA AND EURASIA

A number of families in Scrophulariales, e.g., Myoporaceae, Pedaliaceae, Selaginaceae, Stilbaceae, and Retziaceae, exhibit a clearly southern distribution; in Scrophulariaceae itself there are entirely or mainly southern tribes such as Aptosimeae, Calceolarieae, Hemimerideae, Manuleae, and Aragoeae (Hong & Nilsson, unpubl.). Some mainly northern tribes also have well-developed southern elements; for example, the *Hebe* complex and the genus *Detzneria* of Veroniceae in Australasia, and *Lamourouxia* and *Euphrasia* of Rhinantheae in Australasia and South America. Many tropical and southern genera in the family are disjunct, e.g., *Bacopa, Linderia, Gratiola, Stemodia,* and *Buchnera* in Africa, Asia, Australia, and America; *Striga* and *Limnophila* in Africa, Asia, and Australasia; and *Hebe* and *Jovellacea* in Australasia and South America. On the basis of this distribution, it is reasonable to suggest that the Scrophulariaceae originated and differentiated rather early, probably when Pangaea was still extant or at least before Gondwana had broken up. As to North American/eastern Asian distributional pattern, shown by the genera *Penstemon, Orthocarpus, Mimulus,* and *Veronicastrum,* it is quite plausible that they migrated from North America to Asia or vice versa through Beringia before the

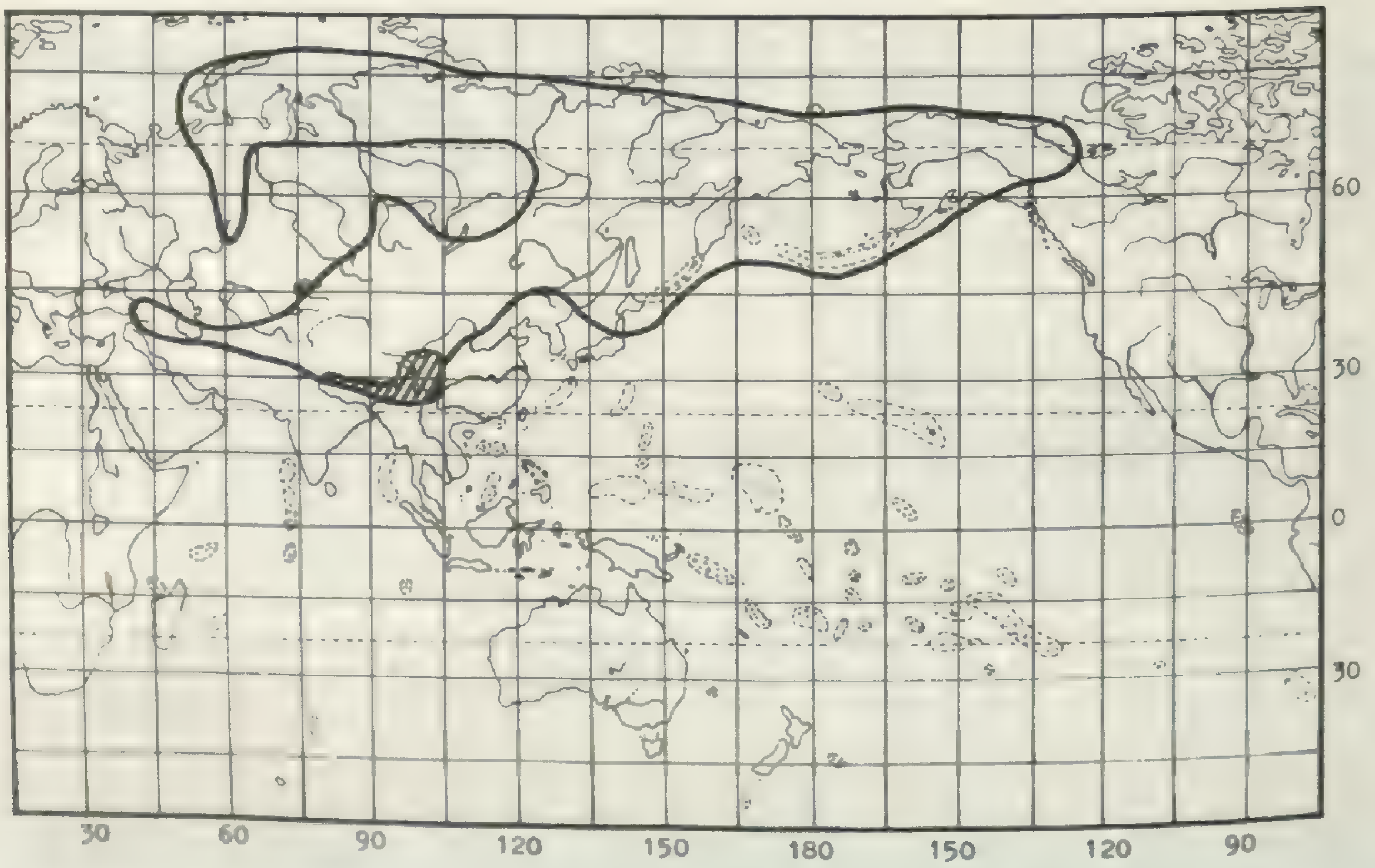

FIGURE 12. Distribution of *Lagotis.* The distribution center is indicated by the shaded area. Only one species, *L. glauca,* extends into North America.

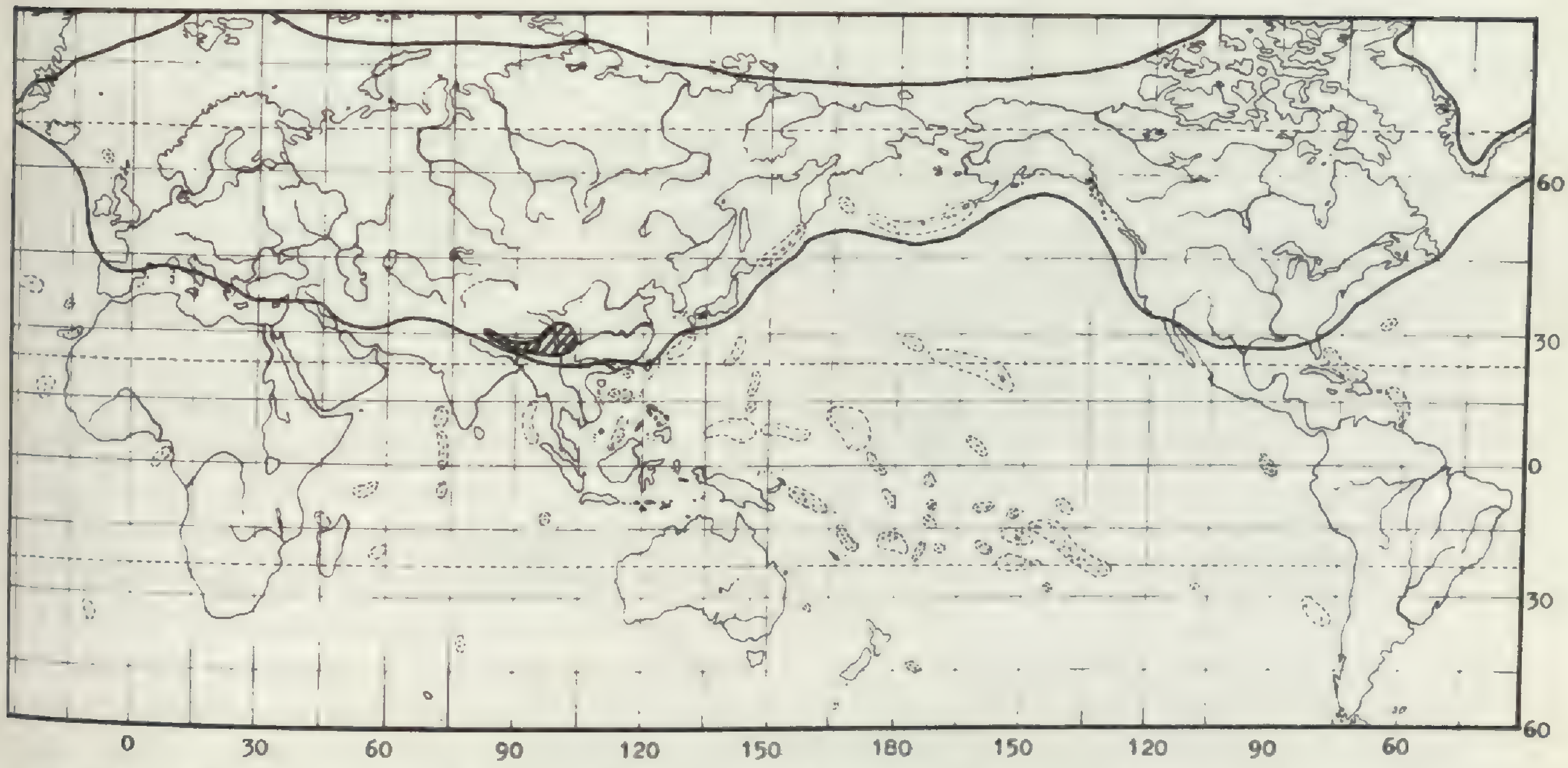

FIGURE 13. Distribution of *Pedicularis*. The majority of species (ca. 300 out of 500) grow in the area shaded.

end of the Miocene, i.e., some 12 million years ago, when the climate there was temperate or cool-temperate (Wolfe, 1972). In pattern 4, represented by genera with a more or less continuous distribution through the Bering Strait and the Aleutians, migration via these two routes during the Quaternary can hardly be doubted.

From the foregoing, floristic migration between Eurasia and North America may have taken place in three phases. The exact time of the earliest one is still vague, either when Laurasia was still extant, or later, but when the climate around Beringia was warm-temperate or temperate (probably before Early Miocene); the time and route of the second one is rather certain, i.e., through the Beringian region when it was temperate or cool-temperate; the third is even more certain, through the Bering Strait or the Aleutians in the Quaternary.

MIGRATIONAL DIRECTION

Despite the difficulty in answering the question of migrational direction, I would, nevertheless, like to speculate about it and suggest hypotheses. There is not enough information available for

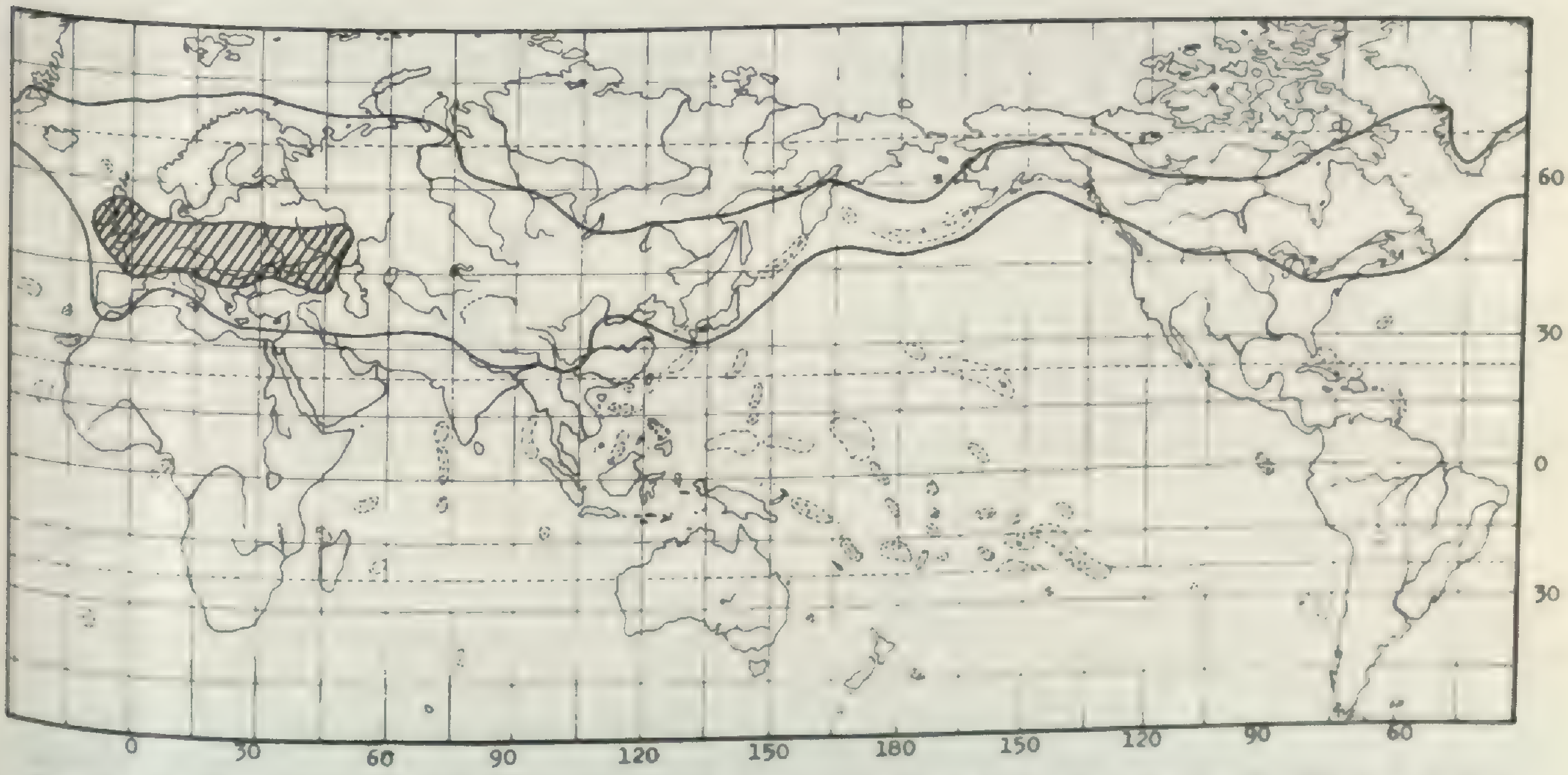

FIGURE 14. Distribution of *Euphrasia* section *Euphrasia*. Shaded area indicates the distribution center.

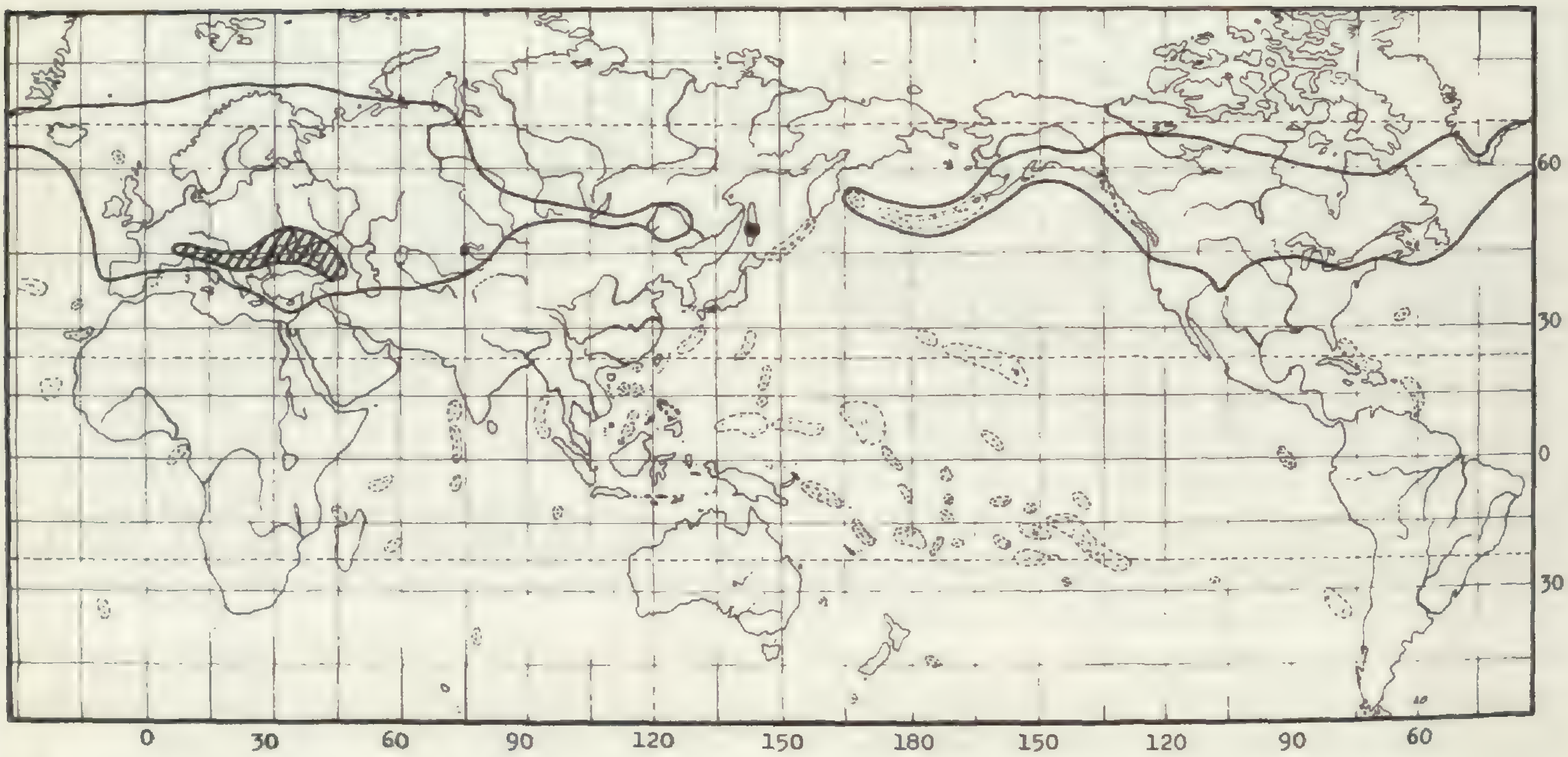

FIGURE 15. Distribution of *Rhinanthus.* The distribution center is indicated by the shaded area.

determining the center of origin and direction of migration of the tribes Scrophularieae and Antirrhineae, but I can say something about the Veroniceae and Rhinantheae. Of the 24 genera of Rhinantheae, eastern Asia has 14, of which seven are endemic. There are also 14 genera in the tribe in Europe and the Mediterranean region, but only three are endemic. In western and central Asia occur ten genera of the tribe, only one of which is endemic. In North America as a whole there are only eight genera, two of which are endemic, and the two other are concentrated there.

Recently, a new genus of Rhinantheae, *Pseudobartsia,* was described from Yunnan, southwest China (Hong, 1979). A certain number of primitive characters are retained in this genus. The upper lip of the corolla, for example, is almost straight with the two lobes only half-coherent, and has not developed into a definite galea. The seeds are ellipsoidal with a reticulate seed-coat. Therefore, eastern Asia possesses the

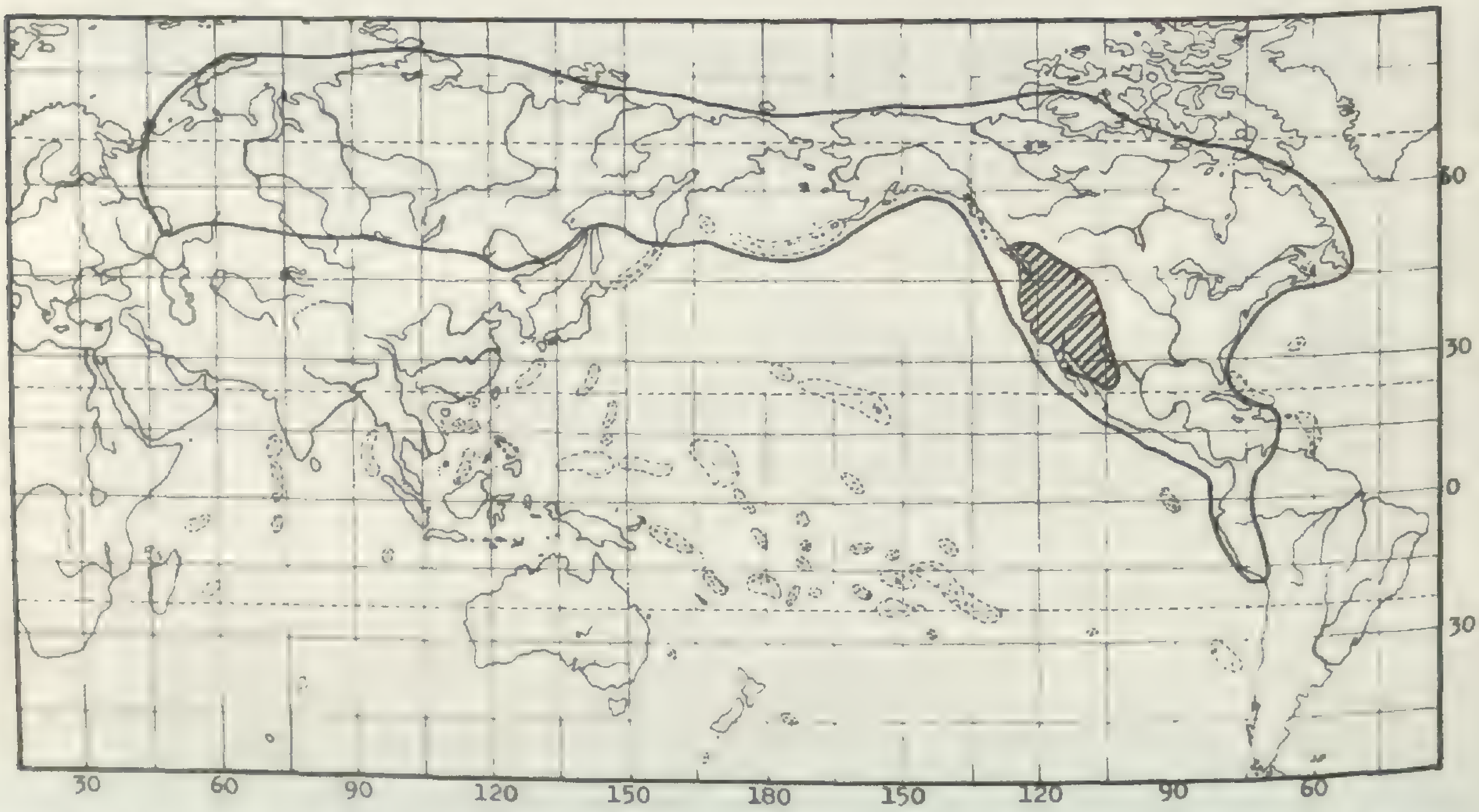

FIGURE 16. Distribution of *Castilleja,* with the center indicated by the shaded area. Only three species occur in northern Asia and northeastern Europe.

most genera, the most endemic genera, and also probably the most primitive element of the Rhinantheae. The two endemic genera, however, and the two highly developed genera in North America, *Castilleja* and *Orthocarpus,* where the upper lip of the corolla is long and navicular, and the lobe tips of lower lip in *Orthocarpus* are sac-like, seem to be specialized elements in the tribe; the monotypic genus *Schwalbea* has its closest relative in eastern Asia. All these facts may indicate that the tribe Rhinantheae originated in eastern Asia and its members in North America are derived. Among 15 northern genera of the tribe Veroniceae, 13 occur in temperate Eurasia and nine of them are endemic to the region. All the primitive members of the tribe but *Detzneria,* a New Guinea genus, are here. The two endemic genera in North America, *Synthyris* and *Besseya* are, however, closely allied to *Veronica* and are apparently derived (Hong, 1984). Figure 17 shows the distribution of the genus *Veronicastrum* as an example of migration of scrophulariaceous plants from eastern Asia to North America.

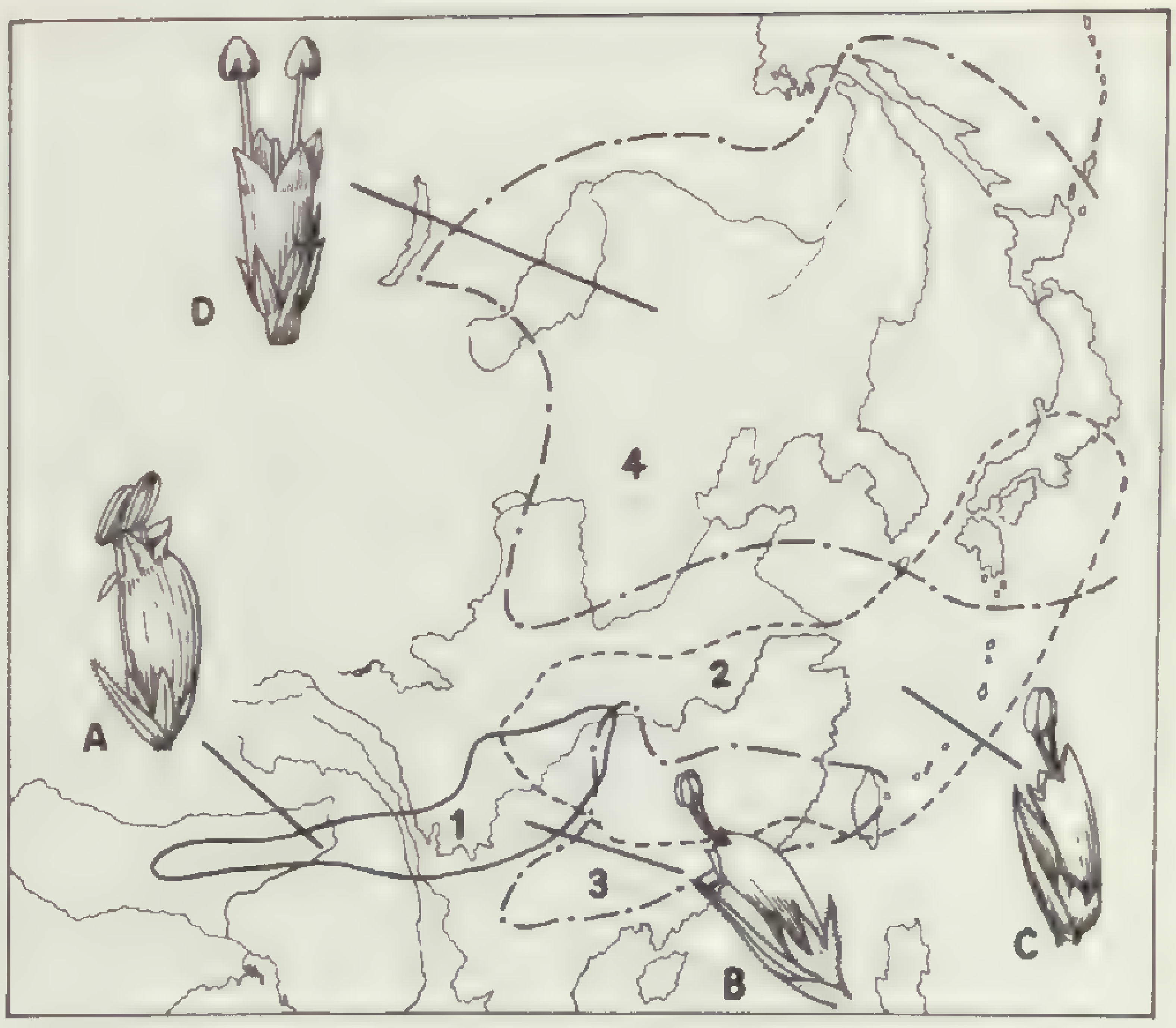

FIGURE 17. Distribution of the sections of *Veronicastrum,* showing the plausible relationship between migration and corolla evolution. 1. Section *Calorhabdos* (Benth.) Hong. 2. Section *Plagiostachys* (Franch.) Yamazaki. 3. Section *Pterocaulon* Yamazaki. 4. Section *Veronicastrum.*

The migration during glaciation from eastern Asia to North America through the Bering Strait of *Pedicularis, Euphrasia, Lagotis, Veronica,* and *Rhinanthus* is almost certain. All eight sections and most of the species of *Veronica* occur in temperate Eurasia, especially in the southwestern part of eastern Asia. All 13 native species, apart from the cosmopolitan species, of the genus in North America are those adapted to cool or mountainous conditions and belong to three rather advanced sections, *Veronicastrum, Veronica,* and *Beccabunga.* Of these 13 species, four are common to the extreme northeastern part of eastern Asia. *Lagotis* has only one species, *L. glauca,* in Alaska, Yukon, and the adjacent region of Canada, which also grows in Kamchatka and Sakhalin. The other genera have similar patterns.

Was plant migration between eastern Asia and North America unidirectional, i.e., only from the former to the latter? Has the opposite migration ever taken place and, if so, to what extent? According to what has been stated earlier, the following four genera may be such cases. *Penstemon* is centered in southwest North America, with only one species extending into central America, and a single species, *P. frutescens,* in Kamchatka, the Kuriles, northern Japan, Sakhalin, and the Okhotsk region (Fig. 7), where it has no close relatives. The disjunct occurrence may be the result of migration from western North America through Beringia before the Late Miocene, when the Bering Strait had not opened (Durham & MacNeil, 1967) and the climate there was temperate or cool-temperate. *Orthocarpus,* which is centered in the Pacific Coast states, may represent another example of the migration from western North America to eastern Asia. The only Asian species of the genus, *O. chinensis,* was described recently from a single specimen collected half a century ago from central China. No additional collections have been made. The migration from western North America to eastern Asia of *Castilleja,* which also has western North America as its distributional center and has only three species in northern Eurasia, is also presumed by Yurtsev (1972). The case of *Mimulus* is more difficult to explain. In spite of its wide distribution in tropical Africa, Australasia, eastern Asia, and America, it is best developed in western North America, where nine of the ten sections and over two-thirds of the species occur. All seven species in eastern Asia except *M. strictus* (in northern India and northern Pakistan and conspecific with African plants, and may well indicate another source) belong to the section *Paradanthus,* which is also highly centered in western North America. The Asian species, except *M. strictus,* are very closely related to each other and also to those of the Pacific Coast states; for example, *M. sessilifolius* in Japan to *M. dentatus* on the Pacific Coast, and the Asian *M.*

tenellus to the western North American *M. inconspicuus* (Grant, 1924). Another fact connected with the immigration of Asian species from western North America is that the *M. tenellus* complex exhibits a challenging taxonomic problem in southwestern China and the eastern Himalayas, where numerous local races and variants occur.

It is usually suggested on the basis of mammals and some other plant groups that migration from Asia to North America was much more intensive than in the opposite direction (Yurtsev, 1972). The conclusion does not seem to hold true as far as the scrophulariaceous plants are concerned. Six genera, *Euphrasia, Lagotis, Pedicularis, Rhinanthus, Veronica,* and *Veronicastrum,* are suggested to have migrated from eastern Asia to North America, but four genera, *Castilleja, Mimulus, Orthocarpus,* and *Penstemon,* may have migrated in the opposite direction. Although *Linaria, Melampyrum,* and *Scrophularia* may have migrated from Eurasia to North America, it is doubtful if the event took place from eastern Asia to North America through Beringia. *Antirrhinum* presents an even more difficult case in this respect.

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A COMPARISON OF ORCHID FLORAS OF TEMPERATE NORTH AMERICA AND EASTERN ASIA[1]

CHEN SING-CHI[2]

ABSTRACT

A phytogeographic analysis is made of the orchid floras of temperate North America and eastern Asia. The relationships between them are shown characteristically by the disjunctive patterns of distribution in the eight species-pairs of *Cypripedium, Listera, Pogonia, Liparis,* and *Platanthera,* as well as in some other genera such as *Tipularia, Arethusa* (*Eleorchis*), *Aplectrum* (partly *Cremastra*), and *Tropidia,* in the two continents. Data of these distribution patterns support an assumption that the discontinuous distribution in orchids between temperate North America and eastern Asia is the result of migration via the Beringian link, or by way of the northern Pacific, but this was not necessarily the only migration route concerned.

The Orchidaceae is an advanced family with minute seeds that can be dispersed effectively by wind over long distances. Because there are so few nutrients in the seeds, their distribution is restricted by ecological conditions. There are a number of closely related orchids extensively or disjunctively distributed between temperate North America and eastern Asia; among them, species pairs are most interesting. These pairs are similar in morphology to the extent that most previously have been considered as conspecific. Although such morphological similarities do not necessarily indicate genetic relationships, they often do. No attempt is made here to further examine the question of their evolutionary relationship, which would require investigations using other approaches, especially cytogenetic research. The purpose of this paper is to discuss how present distribution patterns have been developed.

FLORISTIC COMPARISON

There is a striking similarity between temperate North American and eastern Asian orchid floras. In the latter area, however, there occurs a large number of taxa, including many endemics and primitive forms.

A total of 106 species with many varieties in 23 genera are reported to occur in temperate North America (Correll, 1950; Luer, 1975), whereas in eastern Asia there are about 350 species grouped into 80 genera, of which 62 genera including 15 species occur in Japan (Ohwi, 1953). Among them, 16 genera are common to both continents: *Cypripedium, Cephalanthera, Epipactis, Listera, Pogonia, Spiranthes, Goodyera, Orchis, Coeloglossum, Platanthera, Habenaria, Liparis, Malaxis, Corallorhiza, Tipularia,* and *Calypso* (excluding *Aplectrum* and *Arethusa*). Consequently, more than two-thirds of the total orchid genera of temperate North America show a phytogeographic link with eastern Asia. No single genus is found exclusively in North America and Europe, whereas there are several strictly Eurasian genera such as *Neottia, Epipogium, Herminium, Neottianthe, Gymnadenia,* and *Peristylis.*

Few epiphytic orchids are found in North America except in southern Florida and coastal and southern Mexico, whereas in China several genera of epiphytic orchids occur south of the Qin Ling Mountains: *Coelogyne, Pholidota, Pleione, Ischnogyne, Liparis, Dendrobium, Eria, Oberonia, Holcoglossum, Cleisostoma, Vanda,* and *Taeniophyllum.* Some grow as far north as about 34° to 36°N latitude. Examples are *Liparis fargesii* Finet (33°55′N), *Dendrobium hancockii* Rolfe (33°55′N), and *Cleisostoma scolopendrifolium* (Makino) Garay (36°N) (Chen & Tang, 1982).

High endemism in eastern Asia is notable. Seven genera, *Tangtsinia, Diplandrorchis, Changnienia, Stigmatodactylus, Ephippianthus, Dactylostalix,* and *Neofinetia* (not including *Eleorchis* and *Kitigorchis*), are confined to eastern Asia, whereas three, namely *Hexalectris, Calopogon,* and *Isotria,* occur only in temperate

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North America. In addition, eastern Asia has more subendemic genera such as *Bletilla, Hemipilia, Porolabium, Amitostigma, Archineottia, Androcorys, Ischnogyne,* and *Holcoglossum.* The richness of the above-mentioned eastern Asian orchid flora results in part from the wide range of available areas from subtropical to temperate zones, and a number of tropical taxa that have ranges extending northward into this region. However, in North America and northern Africa there is no such range of areas because of the interruption by either ocean or desert, and few tropical orchids there spread northwards as far as in eastern Asia. Similarly, in eastern Asia temperate genera such as *Cephalanthera, Epipactis, Listera, Pogonia,* and *Hemipilia* extend southward to Thailand and Vietnam. In North America, there are no examples of such southern migration of temperate orchids in southern Florida and only a few in Mexico.

More primitive taxa are seen in eastern Asia (Chen, 1982). For example, a primitive genus *Tangtsinia,* possessing a regular perianth, a terminal stigma, and five staminodes, has been reported from southeastern Szechuan, where *Cathaya argyrophylla* Chun & Kuang also was found in 1958. Another primitive genus, *Archineottia,* is characterized by an incomplete column, exhibiting a terminal stigma and an erect stamen with a free filament attached to the back of the column. The columnar structure found in this genus and the allied *Neottia* is transitional from one form with a stamen not fully adnated to the style to another in which fusion is complete. The genus consists of four species, two in China and one each in Sikkim and northern India. Its ally, *Diplandrorchis,* possesses two stamens that are opposite the dorsal sepal and the median petal (lip) respectively. These orchids belong to the subtribes *Neottinae* and *Limodorinae,* both having suspensorless embryo and relatively large chromosomes, characters also found in the *Cypripedium* group and some other primitive taxa. Additionally, many other primitive genera such as *Apostasia, Cephalanthera, Sinorchis, Aphyllorchis,* and *Pogonia,* also are found in eastern Asia.

Distribution Patterns

The distribution patterns of the orchids indigenous to North America and eastern Asia can be divided into the following four categories:

Continuous distribution in the northern Pacific. In this region, a few orchids are continuously distributed from Japan or northern China via the Aleutian Islands to North America. For example, *Orchis aristata* Fisch. occurs in Korea, northern Japan, Sakhalin, Kamchatka, the Aleutian Islands, and the Alaskan Peninsula (Fig. 1); *Platanthera hyperborea* (L.) Ldl. is found in northern Japan, Kamchatka, the Aleutian Islands, North America, Greenland, and Iceland; and *Cypripedium guttatum* Sw. var. *yatabeanum* (Makino) Pfitz. occurs in northern Japan, Kamchatka, the Aleutian Islands, and the Alaskan Peninsula (Fig. 2). However, attention is called to *Platanthera chorisiana* (Cham.) Rchb. f., which is distributed disjunctively in northern Japan, southern Sakhalin, and in the southeastern corner of Alaska and British Columbia, but is absent from the Alaskan Peninsula (Fig. 3).

Disjunctive distribution between eastern North America and eastern Asia. Within this category fall species pairs and individual genera. There are at least eight species pairs found in these two regions. They are similar in morphology and, in most cases, were formerly considered to be conspecific.

Cypripedium is a temperate genus of about 30 species. It is found largely in North America and eastern Asia, with two species extending to Europe. Two species pairs are distributed disjunctively in eastern North America and eastern Asia. *Cypripedium arietinum* R. Br. ranges from Illinois through New York, and Connecticut to Nova Scotia, southern Quebec, southern Ontario, and southern Manitoba; its Asian counterpart, *C. plectrochilon* Franch., occurs in Sichuan, western Hubei, and northwestern Yunnan (Fig. 4). Both species often grow in somewhat boggy and shady places. Another pair is of a slightly wider distribution: the American *C. reginae* Walt. extends as far south as North Carolina and Tennessee, whereas *C. flavum* Hunt & Summerh. is scattered from southeastern Tibet through Yunnan, Sichuan, and Hubei to southern Gansu (Fig. 5). The distribution patterns and environmental conditions of these two species pairs are similar, and both are rather primitive members in the genus. Apparently, the similarities between them are not fortuitous but rather indicate that they have shared a similar historical succession.

The genus *Listera* consists of some 30 species, all found in North America and Asia except for *L. ovata* (L.) R. Br. and *L. cordata* (L.) R. Br., which also extend their ranges to Europe. At least two disjunctive species pairs are generally rec-

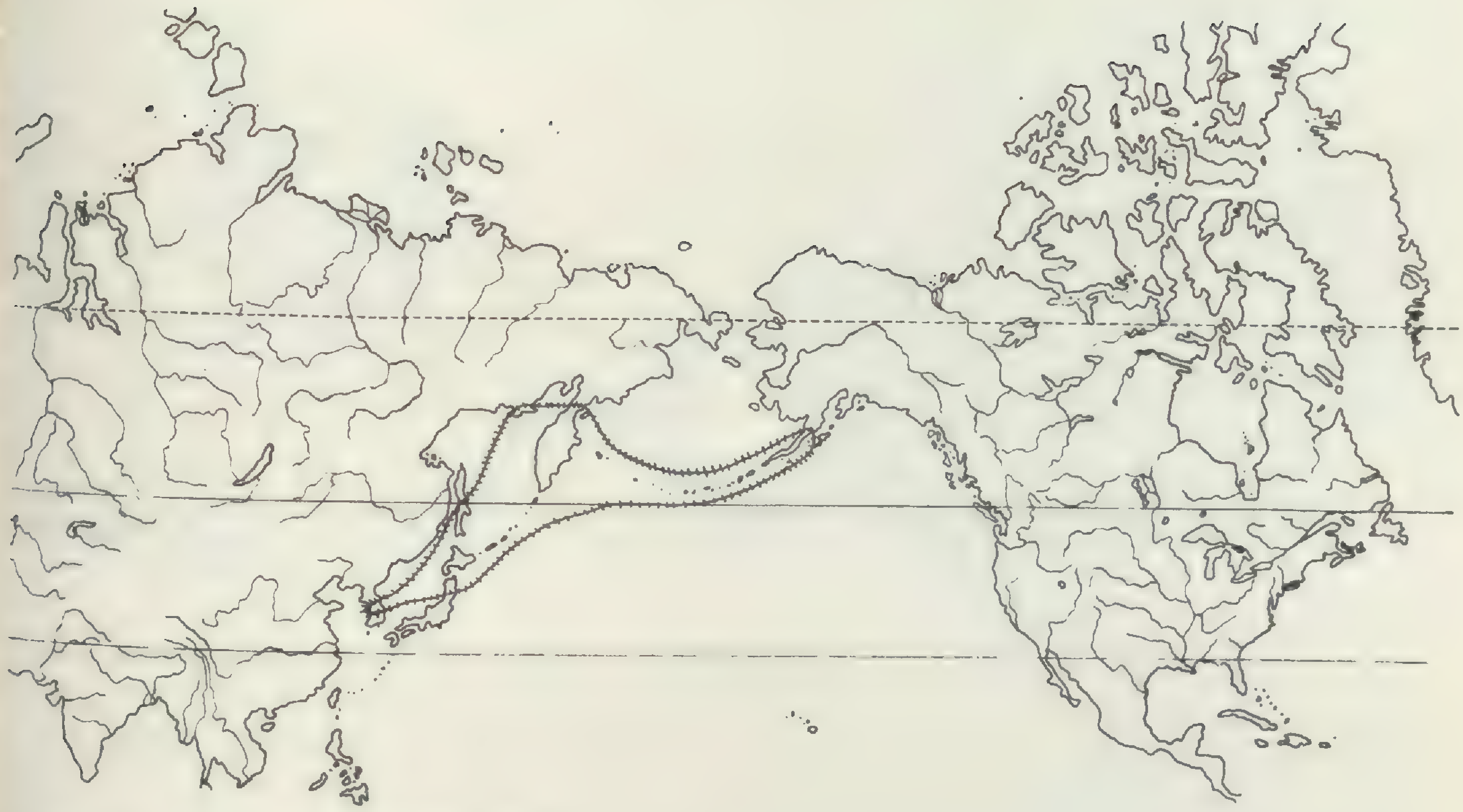

FIGURE 1. Distribution of *Orchis aristata.*

ognized: *L. australis* Ldl. and *L. japonica* Bl. and *L. smallii* Wiegand and *L. nipponica* Makino. *Listera australis* ranges from northern Florida and North Carolina northward to the southern tip of Quebec, whereas its counterpart is confined to Japan (Fig. 6). The other American species is narrowly distributed from North Carolina to Pennsylvania, with its equivalent *L. nipponica* occurring in Japan and the far eastern part of the Soviet Union. *Listera nanchuanica* S. C. Chen, a western Chinese species, closely resembles *L. nipponica.* In addition, there are also some similarities between the American *L. borealis* Morong and the Japanese *L. yatabei* Makino, as well

FIGURE 2. Distribution of *Cypripedium guttatum* var. *yatabeanum.*

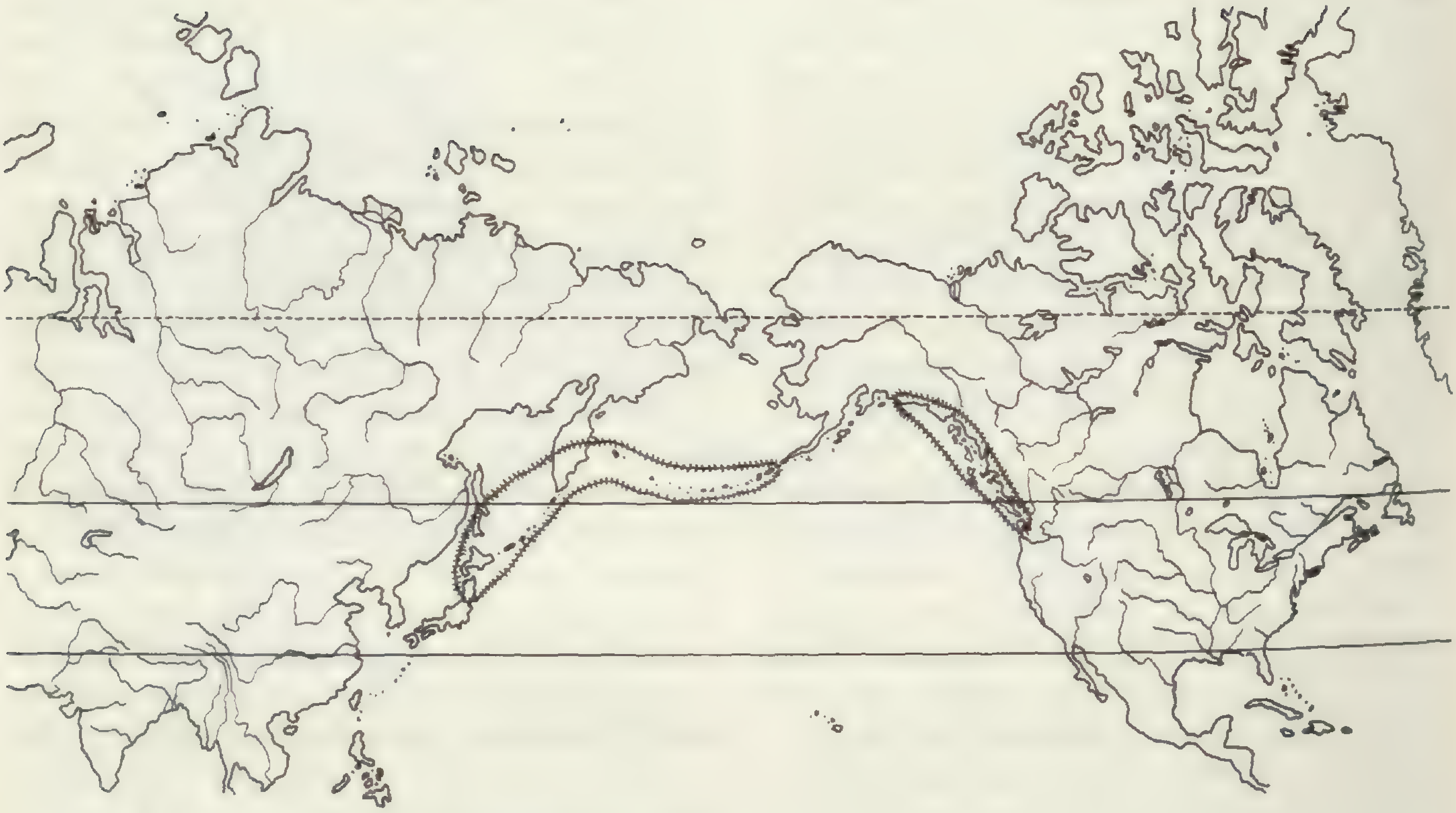

FIGURE 3. Distribution of *Platanthera chorisiana.*

as between the American *L. convallarioides* (Sw.) Nutt. and the Japanese *L. makinoana* Ohwi.

Liparis is a large genus of approximately 250 species. Its epiphytic members constitute the majority, and center in tropical Asia and Oceania. Two terrestrial species occur in temperate North America, and about 25 species, mostly terrestrial, are found in eastern Asia. Among them, *L. lilifolia* (L.) L. C. Richard ex Ldl. and *L. makinoana* Schltr. are similar and constitute a species pair. *Liparis lilifolia* is found in eastern North America from Maine and Vermont along the At-

FIGURE 4. Distribution of the species-pair *Cypripedium plectrochilon* (eastern Asia) and *C. arietinum* (eastern North America).

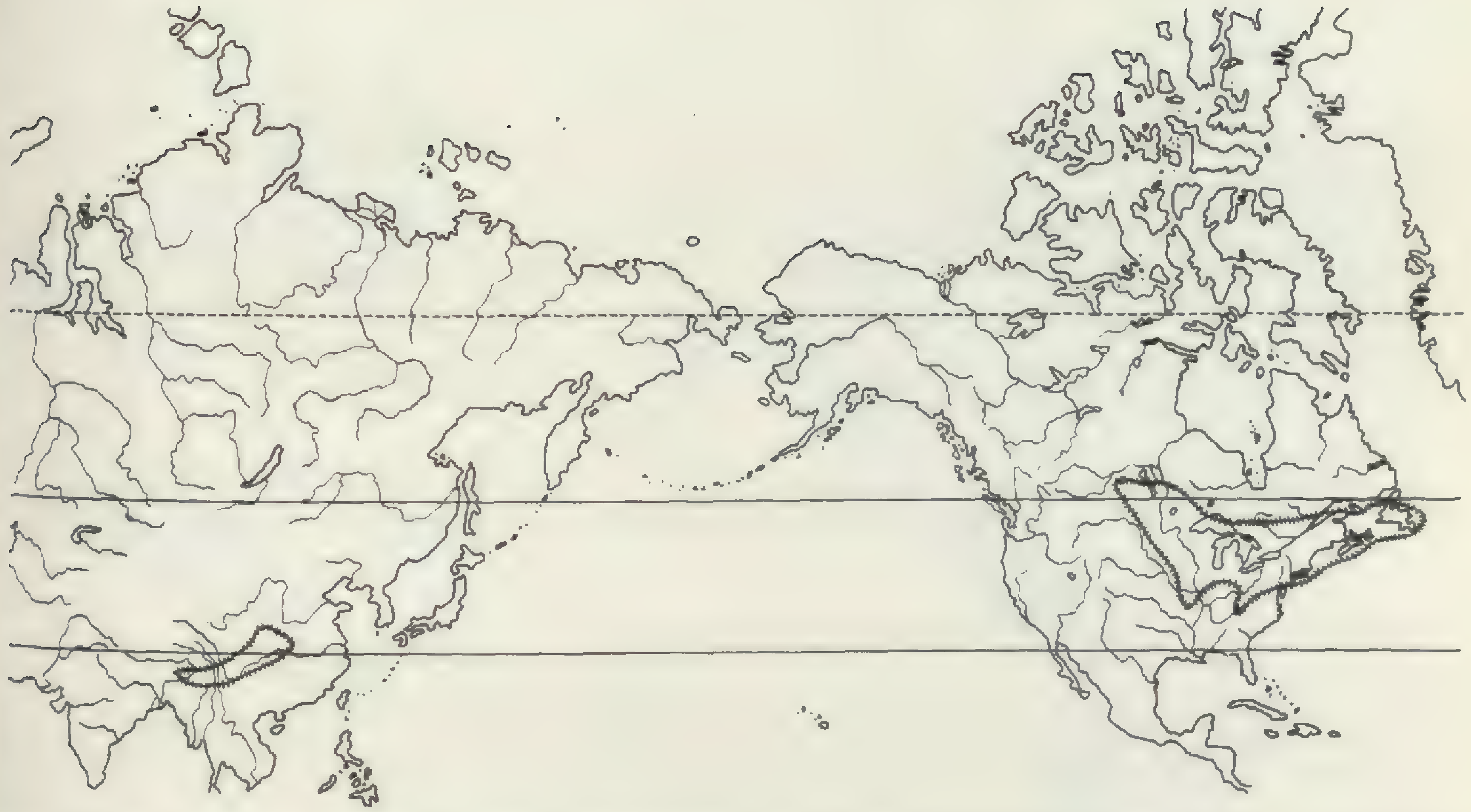

FIGURE 5. Distribution of the species-pair *Cypripedium flavum* (eastern Asia) and *C. reginae* (eastern North America).

lantic states southward to South Carolina, Georgia, and Alabama, and westward through the Central and Lake states to Wisconsin, Minnesota, Iowa, Missouri, and Arkansas, whereas its counterpart is confined to Japan (Fig. 8). Both species are also similar to *L. pauliana* Hand.-Mzt., a species widespread to the south of the Yangtze River of China. Another interesting species is *L. loeselii* (L.) L. C. Richard, which is the only species in the family confined to North

FIGURE 6. Distribution of the species-pair *Listera japonica* (eastern Asia) and *L. australis* (eastern North America).

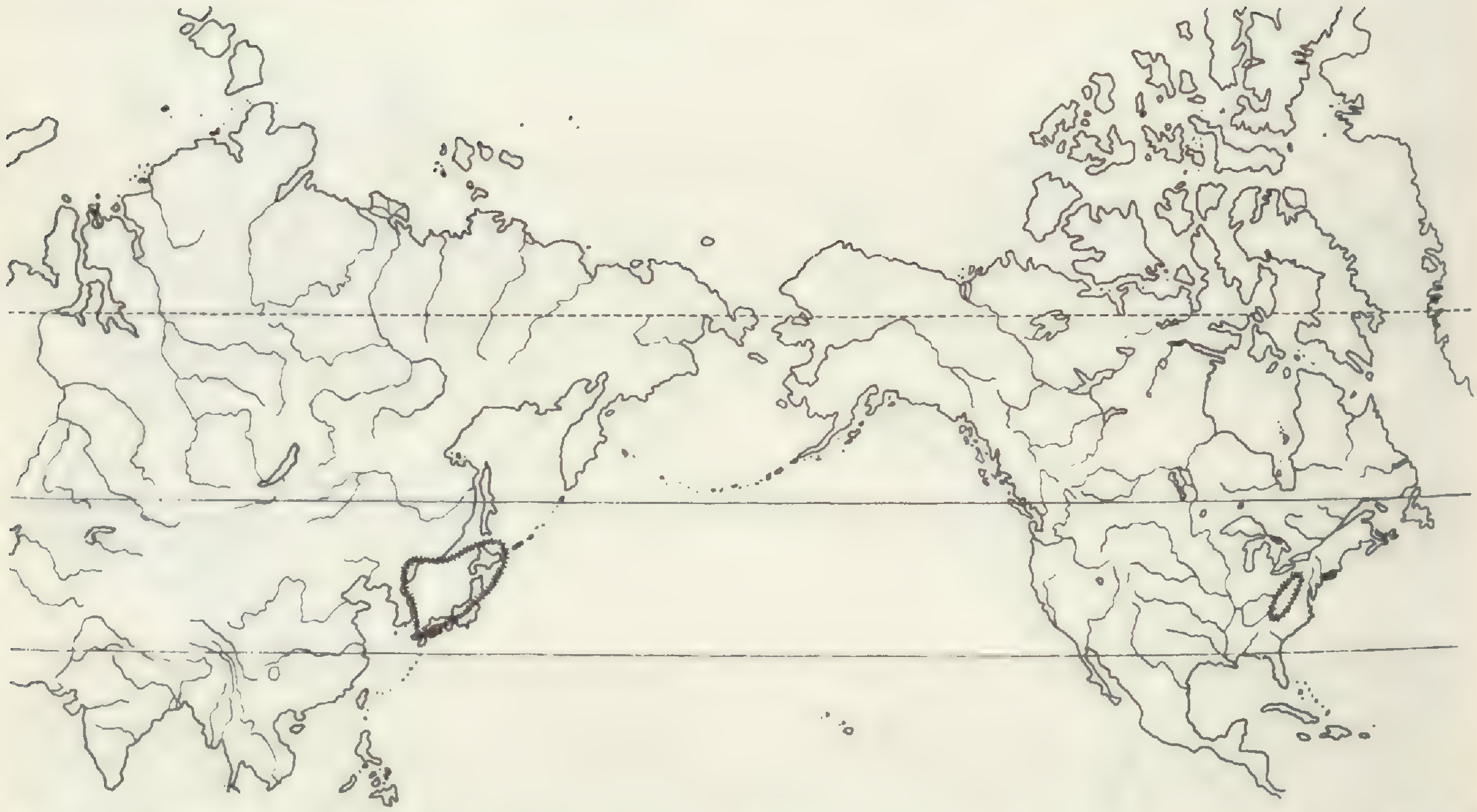

FIGURE 7. Distribution of the species-pair *Listera nipponica* (eastern Asia) and *L. smallii* (eastern North America).

America and western Europe. However, it shows some similarity to a Japanese species, *L. kumokiri* F. Maekawa.

Pogonia has an eastern Asia-eastern North American distribution. *Pogonia ophioglossoides* (L.) Ker-Gawl. is found in eastern North America from Newfoundland to Florida (Fig. 9). The other six species are in Asia, with their southern limits extending to Malaysia. *Pogonia ophioglossoides* is most similar to *P. japonica* Rchb. f., which is widely dispersed from the far eastern part of the Soviet Union and northeastern China

FIGURE 8. Distribution of the species-pair *Liparis makinoana* (eastern Asia) and *L. lilifolia* (eastern North America).

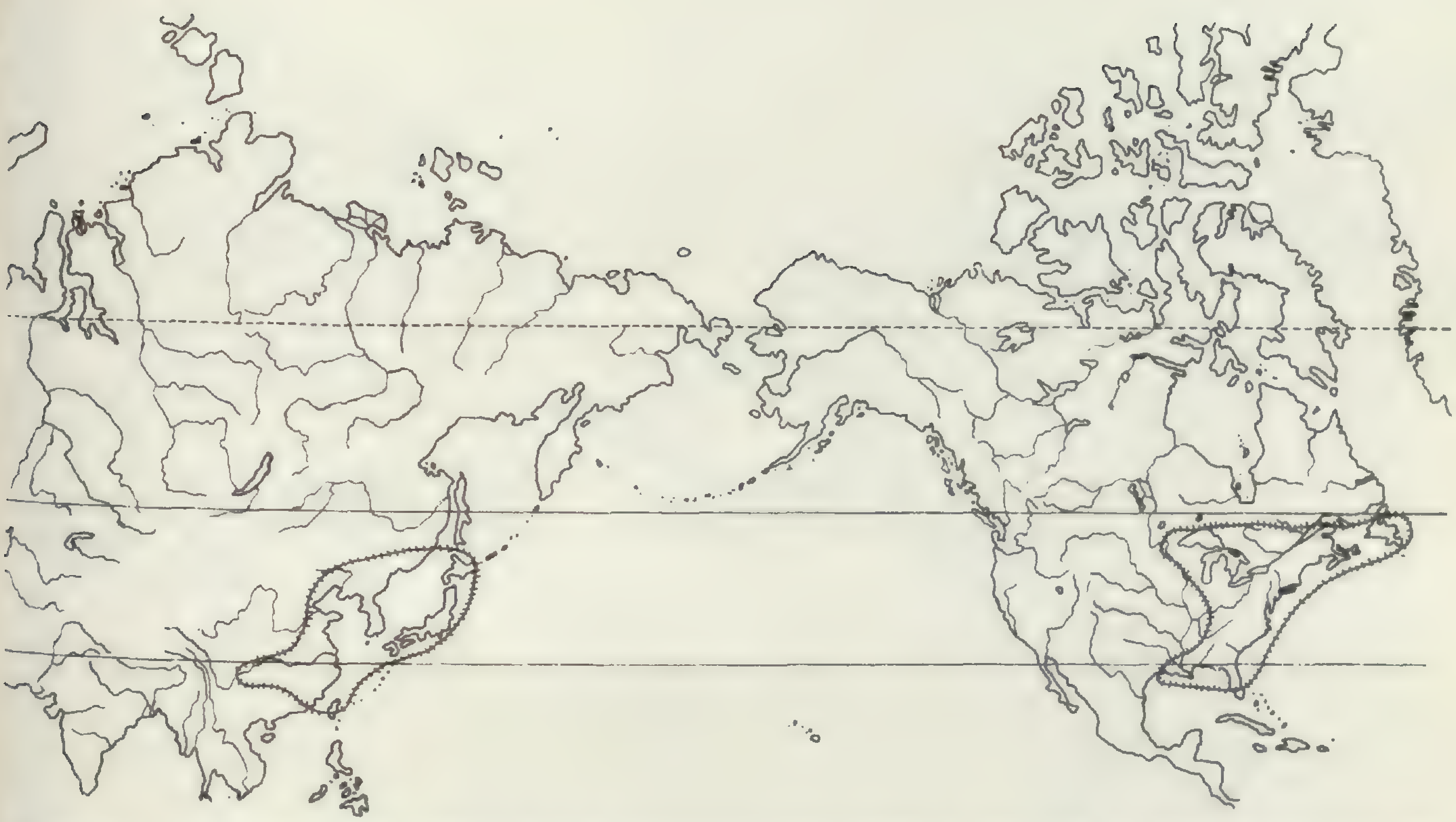

FIGURE 9. Distribution of the species-pair *Pogonia japonica* (eastern Asia) and *P. ophioglossoides* (eastern North America).

through Japan, southward to Jiangsi, Fujian, and Taiwan, and west to Sichuan and Kweichow in China (Fig. 9). *Pogonia* is a primitive genus possessing single pollen grains. In the New World, the genus has three allied genera, *Cleistes, Isotria,* and *Triphora.* These genera formerly were included in *Pogonia,* from which they were separated mainly on the basis of more advanced compound pollen grains occurring in tetrads. In Asia, however, no closely allied genus to *Pogonia* is found.

Platanthera is of worldwide occurrence. Among

FIGURE 10. Distribution of the species-pair *Platanthera florentii* (eastern Asia) and *P. hookeri* (eastern North America).

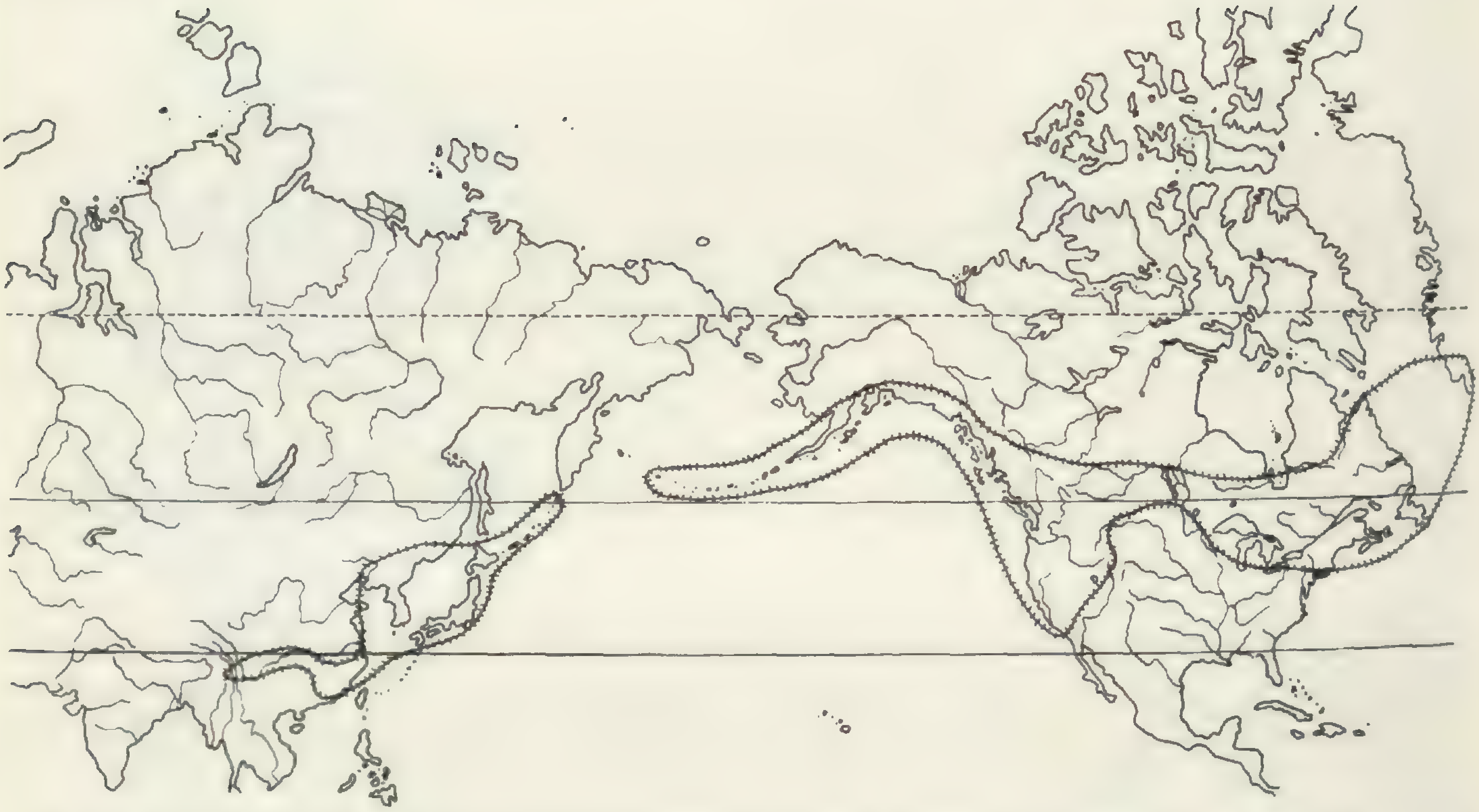

FIGURE 11. Distribution of the species-pair *Platanthera hologlottis* (eastern Asia) and *P. dilatata* (eastern North America).

its 200 species, about 40 are found in eastern Asia, and 36 in North America. The Japanese *P. florentii* Franch. & Sav. closely resembles the American *P. hookeri* (Torrey) Ldl., which occurs in southeastern Canada and the northeastern United States (Fig. 10). Of special interest is another species pair, *P. dilatata* (Pursh) Ldl. ex Beck and *P. hologlottis* Maxim. The former occurs in both eastern and western North America, including the Aleutian Islands, whereas the latter extends from the far eastern part of the Soviet Union southwestward to the Yunnan in China (Fig. 11). These species show a transition from the continuous distribution of same species to the disjunction of species pairs between eastern North America and eastern Asia.

In addition to *Pogonia,* there are three more genera that are confined to eastern North America and eastern Asia: *Tipularia, Arethusa* (*Eleorchis*), and *Aplectrum* (partly *Cremastra). Tipularia* is composed of five species: *T. discolor* (Pursh) Nutt. in southeastern North America, and *T. odorata* Fukuyama and *T. szechuanica* Schltr. in China (one in Taiwan, the other in Sichuan and Tibet) (Fig. 12). The map by Li (1952) includes *Tipularia camtschatica* Spreng., which is not a *Tipularia* but instead a *Platanthera.* The Asian species of this genus are more or less related. However, the American species is rather different from the Asian species with respect to the fugacity of its solitary leaf prior to the appearance of the inflorescence. *Arethusa* and *Aplectrum* each contain two species that are disjunctively distributed in eastern North America and Japan. However, among specialists there are different opinions as to whether the Asian and American representatives are congeneric. Ohwi (1953) considered *Aplectrum unguiculatum* (Finet) F. Maekawa a member of *Cremastra,* and F. Maekawa established in 1935 a new genus *Eleorchis,* based on *Arethusa japonica* A. Gray. However, the close relationship between the two species of each pair are generally recognized.

Disjunctive distribution between western North America and Eurasia. Two closely related genera, *Cephalanthera* and *Epipactis,* demonstrate this particular pattern of distribution. Containing 14 and 20 species respectively, these genera are well represented in Eurasia, each with one species, viz. *Cephalanthera austinae* (A. Gray) Heller and *Epipactis gigantea* Dougl. ex Hook. in western North America. *Cephalanthera austinae* is the only saprophytic member of the genus, which is so unusual in appearance that A. Gray regarded it as a separate genus, *Chloraea. Epipactis gigantea,* scattered from southern British Columbia to Mexico is also unusual in appearance. Neither *Cephalanthera* nor *Epipactis*

FIGURE 12. Distribution of *Tipularia.*

is found in eastern North America except *Epipactis helleborine* (L.) Crantz, which is a common species in Eurasia that was introduced into Canada some 100 years ago. The absence of these two genera in eastern North America could mean that they followed similar historical successions sharing similar ecological conditions.

Disjunctive distribution in the tropical Pacific. In southeastern North America and eastern Asia there are two orchid genera, *Tropidia* and *Erythrodes*, that are disjunctively distributed. *Tropidia* consists of about 20 species, including a single New World species, *T. polystachya* (Sw.) Ames, extending from southern Florida, Mexico, and Central America to the northern end of South America. The remaining members are all tropical Asian and Oceanian, with their northern limits of distribution in Japan (*T. nipponica* Masam.) and Sichuan of western China (*T. emeishanica* K. Y. Lang). *Tropidia polystachya* is different from the rest of the genus except for its slight similarity in habit and inflorescence to those of *T. nipponica*. *Erythrodes* is essentially a New World genus of some 100 species. *Erythrodes querceticola* (Ldl.) Ames is the only species that occurs in North America, extending from Florida to South America. In tropical Asia only a few species of this genus are found, two of which extend northward to China: *E. chinensis* (Rolfe) Schltr. of Yunnan and Kwangdong and *E. latifolia* Bl. of Taiwan and Malaysia. Neither of these genera is found in Africa.

Discussion and Interpretation

It is evident from the foregoing data that the distribution of Orchidaceae between the two continents follows the general rule, although it is an advanced family.

All taxa mentioned above are terrestrial, belonging to different groups, most of which are less advanced members of the family. No epiphytic orchid shows such a pattern of distribution. Although the genus *Bulbophyllum* has a single species occurring in southern Florida (Luer, 1972), and several in eastern Asia, little similarity can be found between them. As a pantropical genus, *Bulbophyllum* consists of more than one thousand species, all of which are epiphytic.

The distribution of the species pairs on two continents often show some similarity and correlation among them. For example, the American species *Pogonia ophioglossoides* is widespread and *Listera smallii* is of local occurrence. Similarly, their Asian counterparts *Pogonia japonica* and *Listera nipponica* are widely and narrowly distributed, respectively. Probably this is due to similar ecological preference and genetic character. However, the American species often show a wider range of distribution and reach

higher latitudes, whereas their Asian allies generally grow at higher elevations. Two species pairs of *Cypripedium* are good examples. The ranges of *C. reginae* and C. *arietinum* extend as far north as 50°N in North America, where they are found at an elevation below 1,000 meters; their Asian counterparts are confined to south of the Qin Ling Mountains (33°–34°N) at an altitude between 1,850 and 3,700 meters.

Phytogeographically, Japan is significant; the aforementioned taxa are found except for *Cypripedium plectrochilon, C. flavum,* and *Erythrodes.* In some cases, species have continuous ranges that extend from Japan or China through coastal areas and continental islands to North America. Examples include *Orchis aristata, Cypripedium guttatum* var. *yatabeanum,* and *Platanthera chorisiana,* although the last species is absent in the Alaskan Peninsula, showing a degree of disjunction in its range. A highly interesting pattern of distribution is exhibited by the species pair *Platanthera dilatata* and *P. hologlottis,* which seem to have been differentiated more recently. Should further climatic changes take place causing their extinction in northwestern North America and northeastern Asia, their distribution would approach that of *Cypripedium reginae* and *C. flavum.*

Thus there is a series of transitions in distributional types; *Orchis aristata* type (continuous distribution in the northern part of the Pacific at the species level); *Platanthera chorisiana* type (distribution somewhat disjunctive in the northern part of the Pacific at the species level); *Platanthera dilatata–P. hologlottis* type (species pairs between North America and eastern Asia); *Listera australis–L. japonica* type (species pairs between eastern North America and western China); *Tipularia* type (disjunctive distribution between eastern North America and eastern Asia at the generic level); and *Tropidia* type (disjunctive distribution in the tropical Pacific at the generic level). It might be assumed from these types that the migration of orchids between these two continents must have taken place repeatedly in different geological times, probably via coastal areas and continental islands of the northern Pacific. The *Orchis aristata* type and the *Platanthera chorisiana* type must represent more recent migration. Slightly earlier would be those of species pairs, such as the *Platanthera dilatata–P. hologlottis,* the *Listera australis–L. japonica,* and the *Cypripedium arietinum–C. plectrochilon* types, but migration does not seem to be as early as the Paleogene. In *Tipularia,* however, the American species shows remarkable dissimilarity from its Asian allies. The morphological differentiation, however, does not necessarily show a direct correlation to the time because the rate of evolution is different in different groups under different environmental conditions. More data and further investigations are necessary.

Furthermore, distribution of some very primitive orchids indicate that there was an ancient connection between these two continents. For instance, *Apostasia* and *Selenipedium* are both relicts and are related to each other in possession of a three-celled ovary, seeds with highly sclerotic and opaque testa, and habits. *Apostasia* is found in tropical Asia, with one species *A. nipponica* Masam., extending to southern Japan, whereas *Selenipedium* is confined to Central America and northern South America. Both the mode of their differentiation and whether or not they are monophyletic is still unknown. However, it seems possible that some subtropical orchids, such as *Tropidia* and others, had migrated through Beringia. During the Eocene, as pointed out by J. A. Wolfe (1972), tropical forests did exist in Alaska. At the same time, the subtropical zone had reached as far north as 42°N in China (Hsü & Li, 1980), and subtropical forests seem to have covered nearly the whole of Japan (Tanai, 1972). Such a climate lasted for a long time until the second half of the Pliocene.

The dissimilarity between orchid floras of western and eastern North America is notable. In western North America there are only ten genera, of which only *Cephalanthera* and *Epipactis* are absent from the East Coast. The flora of California, as pointed out by Raven and Axelrod (1978), is characterized by a high degree of endemism. No exception is found in Orchidaceae. For example, *Cephalanthera austinae, Cypripedium californicum* A. Gray, and *Platanthera* sect. *Piperis* all are very distinct taxa, to which no close allies are found in eastern North America and Eurasia.

There is little indication of more recent interchange of orchids between western Europe and North America, although it is generally recognized that, during the Late Cretaceous and early Tertiary, European floras were similar to that of eastern North Amrica, but not to that of Asia (Hallam, 1981). Only one species, *Liparis loeselii,* is exclusively indigenous to eastern North

America and western Europe, whereas many Eurasian species, such as *Epipactis helleborine, Cephalanthera longifolia* (Huds.) Fritsch, *Epipogium aphyllum* (Schmidt) Sw., *Gymnadenia conopsea* (L.) R. Br., *Cypripedium macranthum* Sw., *Listera ovalis* (L.) R. Br., and *Neottianthe cucullata* (L.) Schltr., are not found in North America. It deserves mentioning that *Epipactis helleborine* has grown well and spread rapidly since it was introduced into eastern North America some 100 years ago, indicating that its absence from eastern North America is not due to ecological but to phytogeographical causes.

In summary, the distribution patterns of Orchidaceae, as in most other angiosperms, show close floristic relationships between eastern North America and eastern Asia. Between these two regions there is a series of transitional patterns of distribution from continuous ranges of the same species to disjunctive ones of closely related species pairs and species. It is rational to interpret that the disjunctive distribution between eastern North America and eastern Asia was realized as the result of the migration via Beringian link and the coastal areas as well as through the continental islands, although these were not necessarily the only migration routes. From these data, of course, it seems to be of little significance to assume the time of their interchange, the origin, and the direction of migration, because there are only few fossil records available for the Orchidaceae (only *Protorchis* from the Eocene in Europe is considered to be credible, and the others such as *Paleorchis* and *Orchidacites*, are more or less doubtful), and their genetic relationships are not clear. As an advanced family, however, such data would be of some help in elucidating certain facts concerning the floristic relationships between temperate North America and eastern Asia.

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PHYTOGEOGRAPHIC RELATIONSHIPS OF PTERIDOPHYTES BETWEEN TEMPERATE NORTH AMERICA AND JAPAN[1]

MASAHIRO KATO[2] AND KUNIO IWATSUKI[3]

The pteridophyte flora of North America comprises 325 species (Tryon, 1969) and the non-endemic species among them are referred to four geographic groups: circumpolar, amphioceanic, tropical, and Mexican. Japanese pteridophytes include about twice as many species as the North American, although the Japanese Archipelago is much smaller. The Japanese species are also more complex taxonomically and phytogeographically (Tagawa, 1959; Ohwi, 1965). The distribution pattern of the Japanese ferns is considered to be related to climatic zones by some authors including Nishida (Graham, 1972). They can be arranged roughly in the following phytogeographic groups: circumpolar, Eurasian, trans-Pacific (related to North America), Sino-Himalayan, and tropical Southeast Asian. The phytogeographic relationships between North America and Japan are found primarily in the temperate to boreal species.

Since Asa Gray's time, phytogeographic relationships between eastern North America and eastern Asia have been discussed by many authors for pteridophytes as well as for flowering and non-vascular plants (Hultén, 1958, 1962; Li, 1952; Graham, 1972; Tryon, 1969; Tryon & Tryon, 1973). In spite of the accumulation of data, there still is no complete phytogeographic analysis of the biological relationship between eastern North America and the Far East. The complex geohistory often is taken into account and the floristic comparison often is made rather theoretically. Changes in land and climate in the Northern Hemisphere that have occurred since the Tertiary have given rise to replacement of boreal, temperate, or warm floras in the areas concerned, and have enabled plants to migrate between the North American and Asian continents via the Bering Strait (chiefly dry land in the Tertiary) and Aleutian chain. This migration probably occurred several times and in either eastward or westward directions. Similar events would have occurred in a south to north direction between temperate and tropical regions. Speciation and gene-flow caused by the geographic isolation and reunion might have taken place in both those areas. The fern floras of North America and eastern Asia include identical or related species. Some of the identical species might be younger and widespread in the Northern Hemisphere, whereas some related species might be older and become restricted to either North America or eastern Asia.

Phytogeographic relationships of fern floras result from species migration that is initiated primarily by spore dispersal. Spore viability varies from about a week to more than several years; green spores are especially short-lived compared with non-green spores. It is reported that fern spores resist, to a considerable extent, physical and chemical environmental stress from low temperature, desiccation, UV- and X-rays, and other factors that operate during the transport (Page, 1979). Tryon (1970) argued the effectiveness of long dispersal of fern spores in island fern floras and estimated that "distances up to 300 miles are only a slight barrier to the migration of a fern flora and that a distance of 500 miles is not a significant barrier." In spite of this, most fern species are restricted in distribution and only a limited number have wide ranges. This means that the dispersal or migration of most ferns is regulated by some unknown factors. Page (1979) pointed out that many biotic and non-biotic ecological relations are involved in migration. In his study on genetic features of disjunct fern populations, Klekowski (1972) considered that the long-distance establishment and future evolutionary processes of fern populations are dependent on the mating system (intragametophytic vs. intergametophytic fertilization) and genetic variability as well as geographic reproductive isolation. Our knowledge of the mechanism of spore dispersal and species establishment at a new locality is still insufficient to fully understand the phytogeographic relationships of the fern flora in question, for which further experimental and field studies are desired.

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In this paper the phytogeographic relationships between temperate North America and eastern Asia are examined, based on the presumed taxonomic affinities of the pteridophyte species concerned. In analyzing the similarity between the two areas, it is intended to elucidate 1) the similarity or difference between the two areas, especially in the composition of their floras, and 2) the taxonomic relationship between the apparently identical or vicarious species known in the two areas.

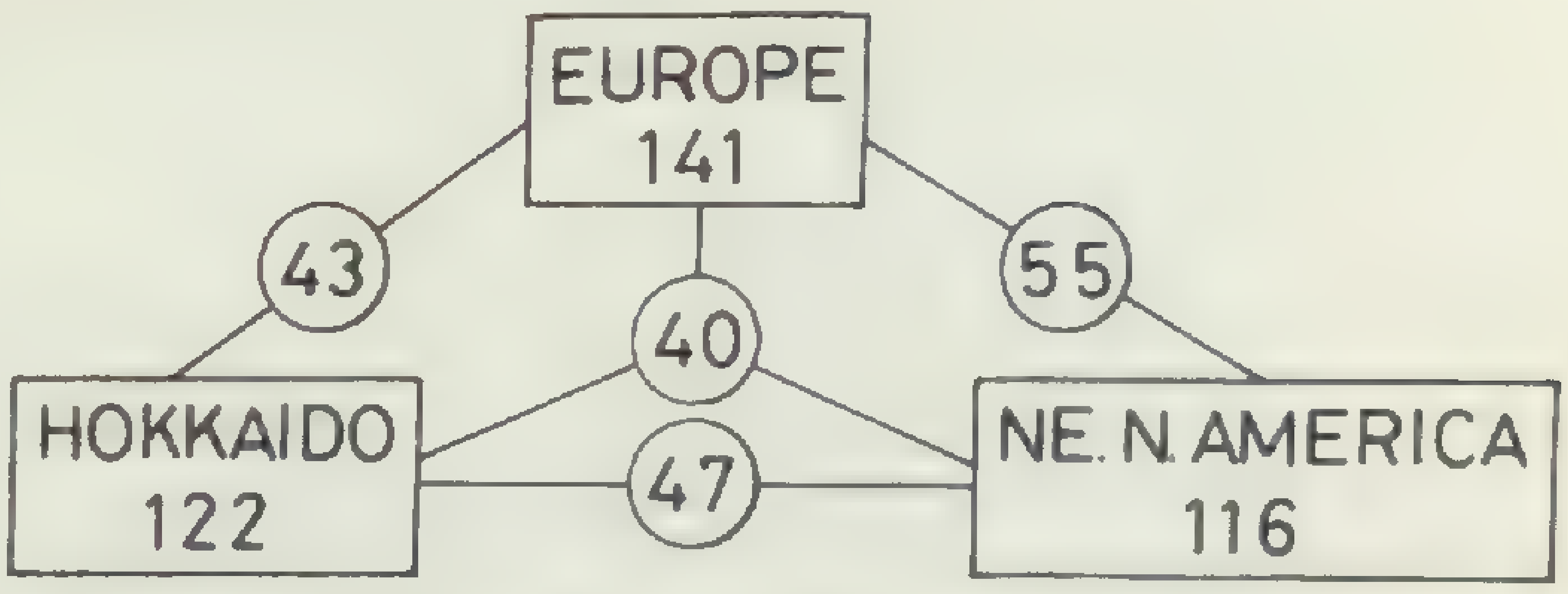

FIGURE 1. The number of common species among Hokkaido, northeastern North America, and Europe. For explanation see the text.

Floristic Similarity

Of 116 species occurring in eastern North America (Morton, 1968) 52 species (45 percent) are also native to Japan, and the figure approaches that for the bryophytes that have the similar dispersal means of airborne spores. Of the 52 common species, 45 species (39 percent) are either widespread in the temperate to boreal Northern Hemisphere or are cosmopolitan, and seven species (cited below) are restricted to eastern Asia, including Japan. The species common to these two areas have their center of distribution in Japan in central and northern Honshu and Hokkaido, whereas southwestern Japan is inhabited by many Sino-Himalayan and Malesian elements. For convenience, Hokkaido will be used for comparisons (Fig. 1). Hokkaido, the northernmost island in Japan of not more than 80,000 km^2, has a temperate to sub-boreal flora. This flora includes 122 pteridophyte species, a number that is almost equivalent to the 116 species in temperate eastern North America. Forty species (33 percent) of the Hokkaido pteridophyte flora have a circumboreal or cosmopolitan distribution (of a possible 45), seven species are of temperate North America–eastern Asian distribution, and 75 species are of other distribution patterns. Including the 40 widespread species, 43 (35 percent) of Hokkaido pteridophyte species are common to those of Europe where 141 species occur (Tutin et al., 1964). Fifty-five species (46 percent) of eastern North American species are distributed also in Europe.

Northwestern North America has a pteridophyte flora consisting of 81 species (Hitchcock & Cronquist, 1955), of which 37 (46 percent) also occur in Japan. Of these, 34 species are circumboreal and three are among the seven species of the eastern North America–eastern Asian distribution pattern.

Li (1952) stated that the distribution patterns of the pteridophytes are different from those of the seed plants that have different means of reproduction and dispersal, and that whereas the floristic relationship of the seed plants between temperate eastern North America and eastern Asia is primarily generic, few fern genera, if any, indicate such a relationship. By contrast, Tryon and Tryon (1973) compared the fern species in both areas and pointed out that the phytogeographic relationship of pteridophytes in both areas is strong and that about 20 percent of the species in eastern North America show disjunct affinities with identical or related species in eastern Asia.

The above floristic comparison shows that most of the apparently identical species (some of which vary infraspecifically) known in temperate North America and Japan are circumboreal and occupy one-third to two-fifths of the pteridophyte flora in every area of eastern North America, Hokkaido, and Europe. The other several species are restricted to both areas in question. The relationships clearly imply a former, more widespread, similar temperate fern flora that was broken by climatic change in the late Tertiary (post-Miocene).

Identical and Vicarious Species

The phytogeographic relationship between temperate North America and eastern Asia is strongly suggested by the apparently identical or vicarious species that are confined to the two areas. The seven apparently identical species are: *Lycopodium obscurum, L. sitchense, Osmunda cinnamomea* (eastern; extending into tropical America as var. *imbricata*), *O. claytoniana* (eastern), *Adiantum pedatum, Onoclea sensibilis* (eastern), and *Polypodium virginianum* (eastern). A few eastern Asiatic pteridophytes extend to the northwestern part of North America, Alaska, and Pacific Canada: *Lycopodium chinense, Selaginella sibirica,* and *Mecodium wrightii.*

Tryon and Tryon (1973) cited examples of several vicarious species between North America

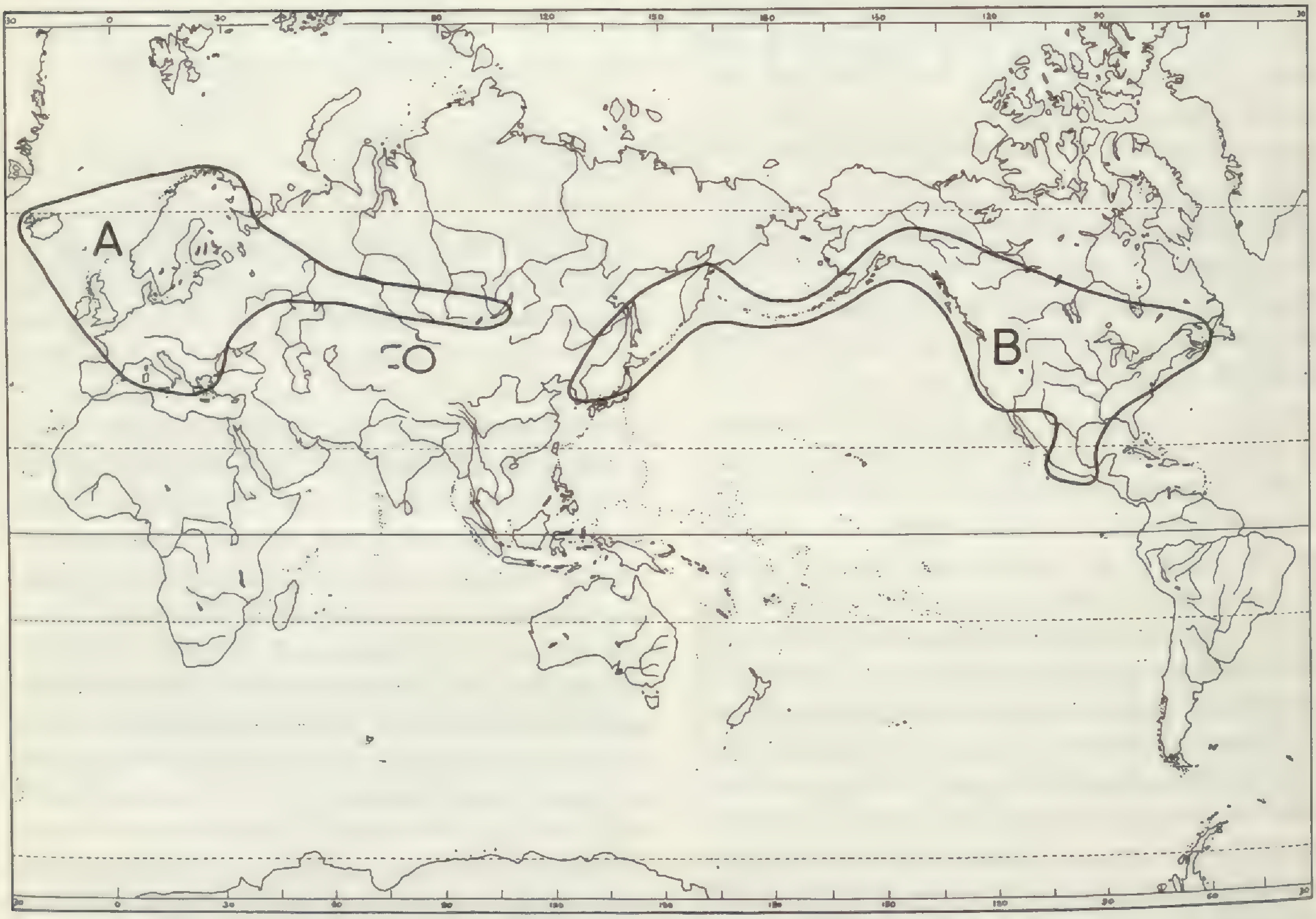

FIGURE 2. Distribution of *Equisetum hyemale.*—A. var. *hyemale*;—B. var. *affine.* (After Hauke, 1963.)

and eastern Asia: *Dennstaedtia punctilobula* of eastern North America vs. *D. appendiculata* and *D. scabra* of eastern Asia; *Thelypteris noveboracensis* of eastern North America and *T. nevadensis* of western America vs. *T. beddomei* and *T. nipponica* of eastern Asia; and *T. simulata* of eastern North America vs. *T. glanduligera* and *T. japonica* of eastern Asia. *Asplenium rhizophyllum* of eastern North America and *A. ruprechtii* of eastern Asia are a well-known example of a vicarious species pair. They are often treated as comprising a separate genus *Camptosorus* because they are typologically different, especially in their reticulate venation, from the other species of *Asplenium.* The following is a discussion of some identical or vicarious species of phytogeographic interest.

Equisetum hyemale. Of the ten species and several hybrids of *Equisetum* that occur in temperate North America, eight are also native to Japan (Hauke, 1963, 1978): *E. sylvaticum, E. pratense, E. arvense, E. fluviatile,* and *E. palustre* of the subgenus *Equisetum* and *E. hyemale, E. variegatum,* and *E. scirpoides* of the subgenus *Hippochaete. Equisetum hyemale* has two varieties, vars. *hyemale* and *affine,* of which the latter shows the North America–eastern Asian relationship. *Equisetum hyemale* var. *affine* is distributed in North America and eastern Asia, whereas var. *hyemale* occurs in Eurasia, extending eastward to Asiatic Russia and westernmost China (Fig. 2). The former variety is considered to have expanded its distribution range in a westward direction (Hauke, 1963).

Hauke (1963) speculated on the phytogeographic evolution of subgenus *Hippochaete,* based on a phylogeny inferred from morphology. It originated in South America and radiated northerly; several species were differentiated in the process. The most primitive member of the subgenus is *E. giganteum,* distributed in South America. An *E. giganteum*-like ancestor likely gave rise to *E. ramosissimum* with two subspecies, the Eurasian ssp. *ramosissimum,* ranging from Europe, Mediterranean Africa, and South and East Africa to Japan, and ssp. *debile* ranging

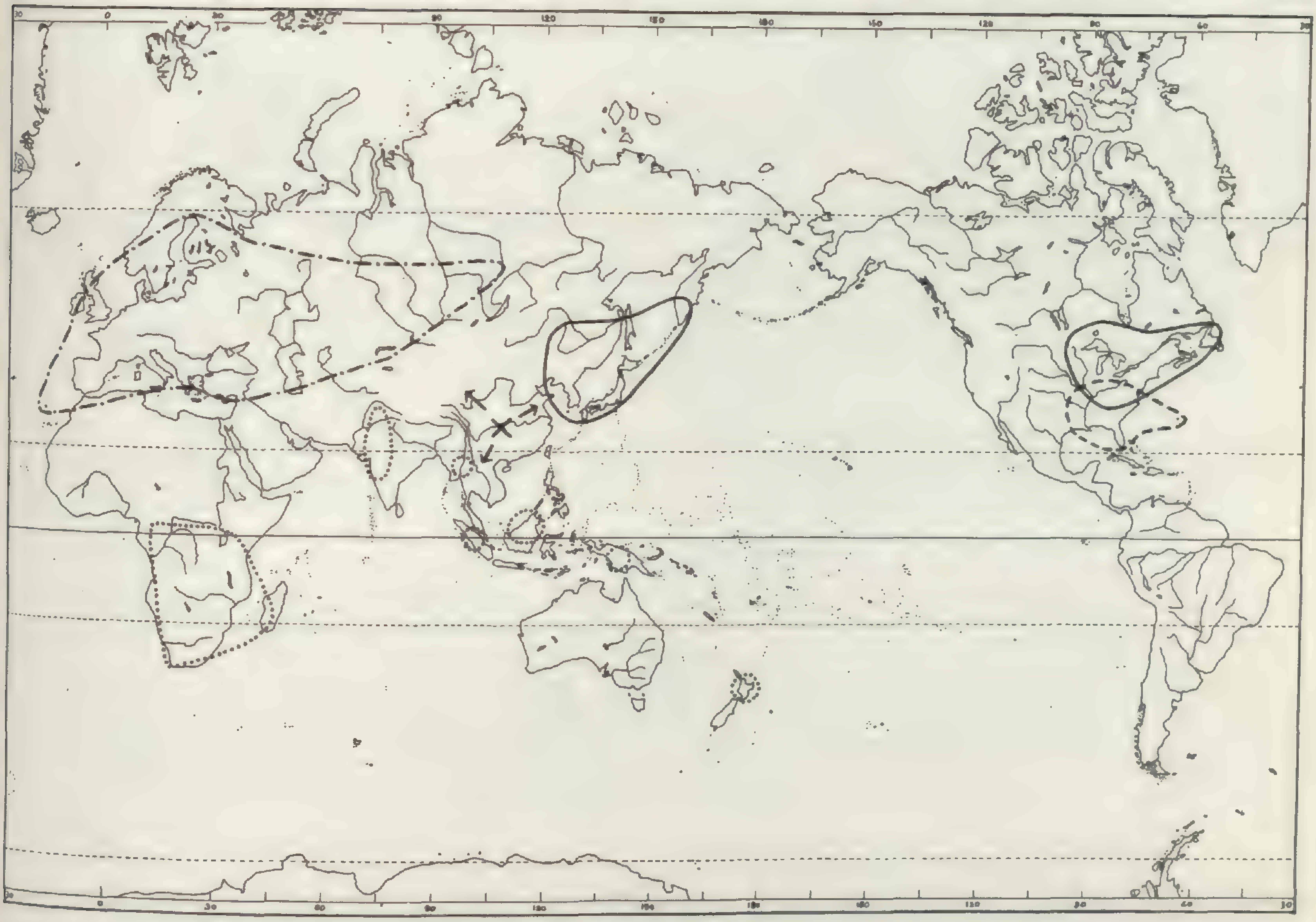

FIGURE 3. Distribution of *Thelypteris palustris*. Solid line, var. *pubescens*; dashed line, var. *haleana*; dotted line, var. *squamigera*; dash and dot, var. *palustris*. (After Tryon, 1971.)

from India to Fiji through Southeast Asia. From the *E. ramosissimum* complex originated two American species, *E. myriochaetum* of Central and South America, and *E. laevigatum* of western North America. "*Equisetum hyemale* developed in southwestern North America, presumably from a common ancestor with the *ramosissimum*-complex, and spread throughout North America. It crossed the North Atlantic land bridge . . . and migrated throughout Europe and across Siberia, there occurring as var. *hyemale*" (Hauke, 1963), whereas var. *affine* crossed the Aleutian chain to eastern Asia.

Thelypteris palustris. This species is worldwide in distribution except in South America (Fig. 3) and is diversified in several characters. It consists of the following four varieties: var. *pubescens* of northeastern North America and eastern Asia; var. *haleana* of the southeastern United States and Bermuda; var. *palustris* of Eurasia; and var. *squamigera* of Africa, India, Burma, Thailand, Sumatra, Borneo, New Guinea, and New Zealand. The classification of this diverse species varies according to the author. Tryon (1971) followed Fernald (1929) in comparing the spore characters of four varieties of *T. palustris*. She suggested that continental southeastern Asia is the center of radiation of this species. It might in turn be suggested that the distribution range of var. *pubescens* has been established by eastward migration from Asia to North America.

Thelypteris noveboracensis and T. nipponica. These two species are often referred to as representing a typical example of vicariants with disjunct distribution (Tryon & Tryon, 1973). *Thelypteris noveboracensis* occurs in eastern North America and *T. nipponica* is distributed in Saghalien, the Kuriles, Hokkaido, northern and central Honshu, Korea, and central and western China. They belong to *Parathelypteris* sensu Holttum and are similar to each other in phenetic features with the exception of the scale features and soral position. The chromosome

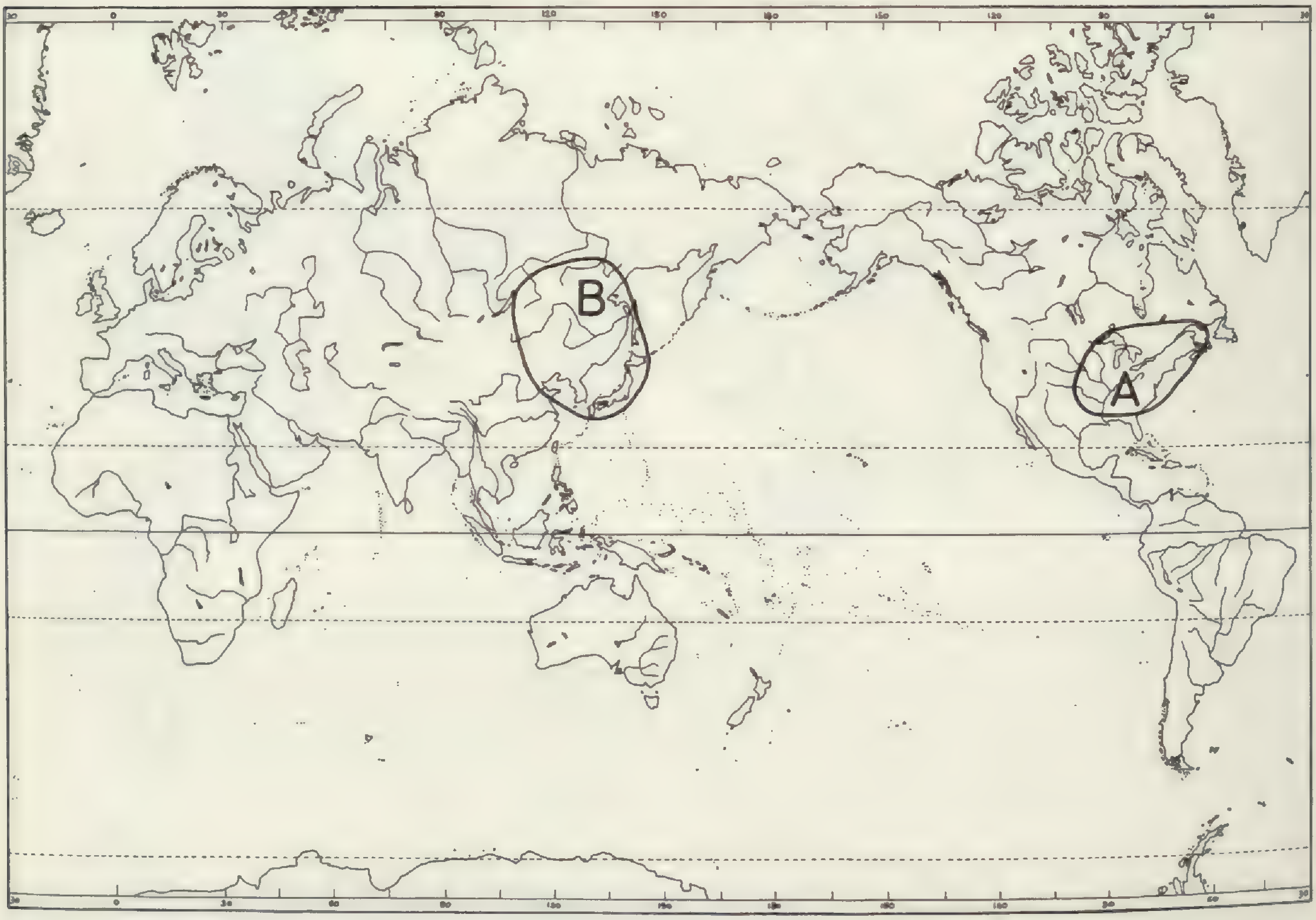

FIGURE 4. Distribution of *Asplenium rhizophyllum* (A) and *A. ruprechtii* (B).

number of *T. noveboracensis* is reported as n = 27 (Tryon & Tryon, 1973) and that of *T. nipponicum* as n = 62 (Hirabayashi, 1970). The latter is often considered to be related to the Asian *T. beddomei*, the chromosome number of which is n = 31, and *T. beddomei* is a suggested vicariant of *T. nevadensis* of western North America. In spite of their phenetic resemblance, it is necessary to revise them, and so we refrain here from discussing the geographic relationship between *T. noveboracensis* and *T. nipponica*. The eastern North American *T. simulata* is also comparable with the Asiatic *T. glanduligera*, although we have no conclusive remarks on the phytogeographic relationship between the two species.

Asplenium rhizophyllum and A. ruprechtii. Asplenium rhizophyllum is known in restricted areas of eastern North America from Quebec to Minnesota, Georgia, Alabama, Kansas, Oklahoma, and Michigan, and *A. ruprechtii* is found in eastern Asia in eastern Siberia, northern and northeastern China, Korea, and Japan (Fig. 4). These species are isolated from the other species of *Asplenium*, especially in their special habit of gemmiferous tips of the simple fronds (often called walking) and anastomosing sagenioid venation; the two species are discriminated by the form of the leaf base. Both often grow on limestone, although they can grow also on non-calcareous rocks. It is certain that these two are closely related, although we have no fossil evidence documenting the migration and speciation of these taxa.

Deparia acrostichoides. The only North American representative of the genus *Deparia* is distributed in the temperate eastern region (Fig. 5). It is closely related to eastern Asiatic vicariants, *D. pycnosora* and allied species of section *Lunathyrium*, differing principally from the latter in possession of creeping rhizomes with more widely spaced leaves. Section *Lunathyrium* has its center of distribution in eastern Asia with many diverse species and therefore it probably

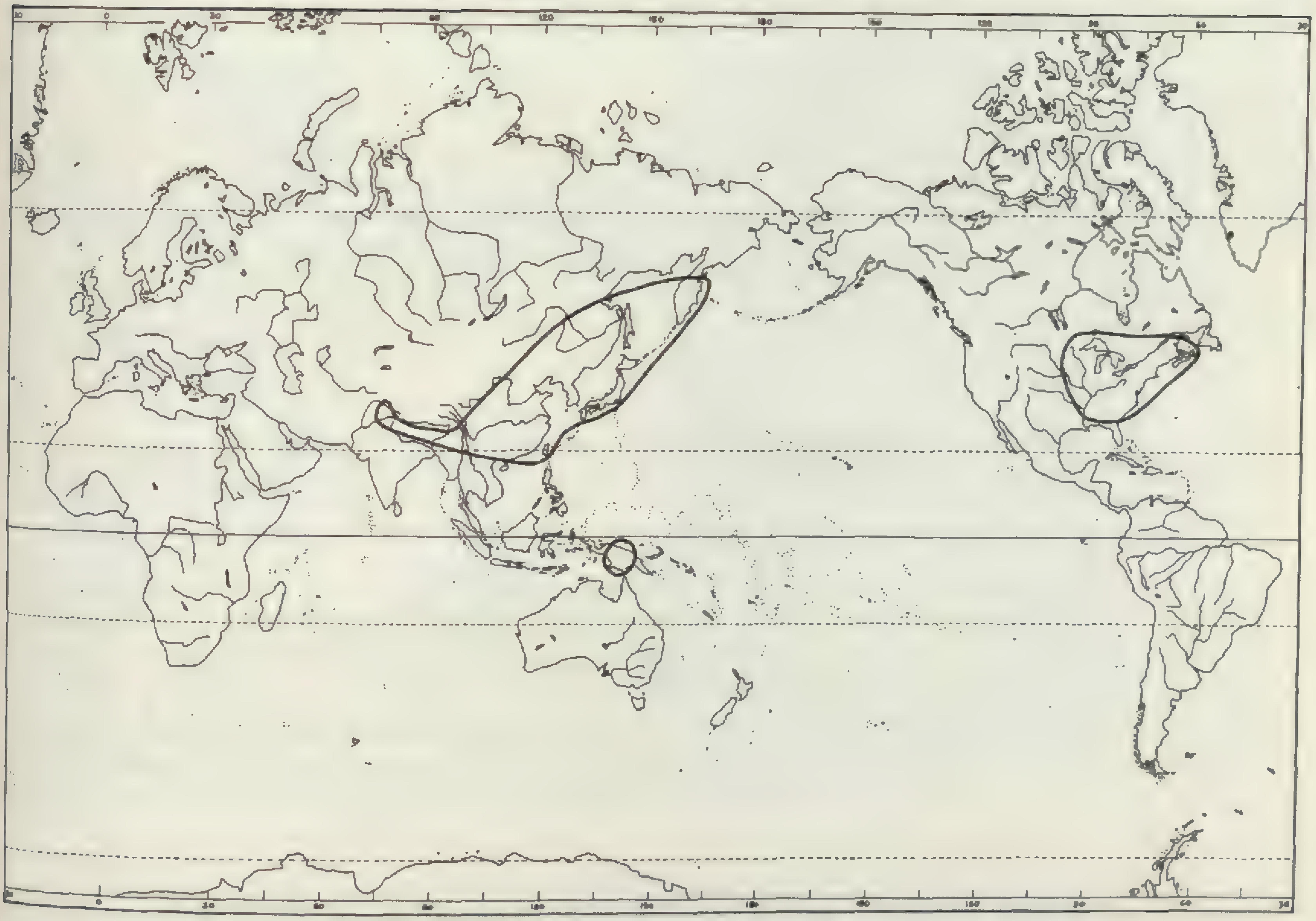

FIGURE 5. Distribution of *Deparia* section *Lunathyrium*. See text for discussion.

originated there. It seems likely that a part of the *D. pycnosora* group migrated in an eastward direction and gave rise to *D. acrostichoides*.

Diplazium pycnocarpon. This species is the only member of *Diplazium* from temperate eastern North America (Fig. 6), although it is still commonly placed in *Athyrium*. It possesses several specialized aspects, including a temperate distribution (in contrast to a tropical and subtropical distribution of the majority of *Diplazium*), and frond morphology (particularly in the veins, which reach the concave pinna margin). *Diplazium pycnocarpon* seems to be, as stated by Tryon and Tryon (1973), a vicarious species of a *D. javanicum* group from east and southeast Asia (Fig. 6), which has usually been segregated as a distinct genus, *Diplaziopsis*, by the imparipinnate fronds, anastomosing veins, and vaulted sausage-shaped sori (Fig. 7). This Asiatic group is in turn closely related to a *D. heterophlebium* group, which has similar anastomosing venation and pinnate fronds without distinct terminal pinnae (Fig. 7), and thereby has been separated as *Dictyodroma* by some taxonomists. Kato (1977) supposed that the *D. javanicum* group and the *D. heterophlebium* group are related to tropical American *D. marginatum* (most often known as *Hemidictyum marginatum*) with a more elaborate reticulate venation (Fig. 7). These species are distinct not only morphologically but also cytologically. It is reported that the basic chromosome number of the *D. javanicum* group and the *D. heterophlebium* group is $x = 41$, a common number of the genus *Diplazium*, whereas *D. pycnocarpon* has $x = 40$ and *D. marginatum* $x = 31$ (Love et al., 1977).

It is possible that *D. pycnocarpon* is derived from a *D. marginatum*-like ancestor, but more likely it was established as a specialized temperate species with a closer affinity to the Asiatic species.

Gymnocarpium dryopteris. The genus *Gymnocarpium* comprises six species that are classified into two subgenera, *Gymnocarpium* of five

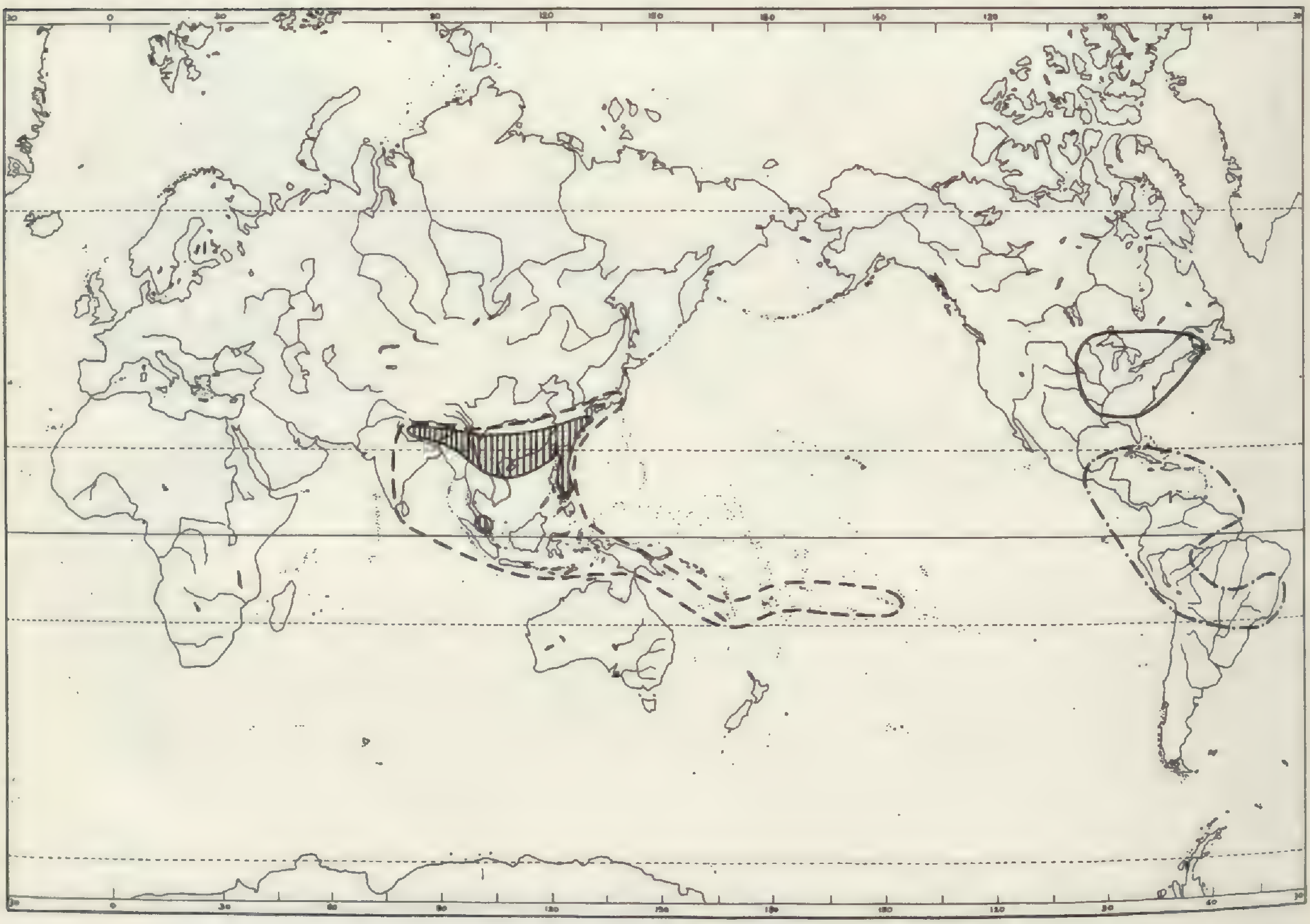

FIGURE 6. Distribution of *Diplazium pycnocarpon* and presumably related species. Solid line, *D. pycnocarpon*; dashed line, *D. javanicum* group (*Diplaziopsis*); vertical lines, *D. heterophlebium* group (*Dictyodroma*); dash and dot, *D. marginatum* (*Hemidictyum*).

closely related species, and *Currania* with one species, *G. oyamense.* Three of the species are restricted to Asia: *G. remote-pinnatum* in Taiwan, *G. fedtschenkoanum* in Tadzhikistan, and *G. oyamense* in Nepal, continental China, Taiwan, Japan, Luzon, and New Guinea, whereas the other three are widely distributed in Asia, America, and Europe (Sarvela, 1978). From its taxonomic relationships and geographic distribution it can be suggested that the genus originated and diversified into two subgenera in Asia and spread to Europe and North America. Cytological studies show that *G. dryopteris* ssp. *dryopteris* has $2n = 160$ and ssp. *disjunctum* $2n = 80$, *G. jessoense* ssp. *jessoense* $2n = 80$, *G. robertianum* $2n = 160$, and *G. oyamense* $2n = 80$ and 160, suggesting that the diversification of the genus arose mostly at the diploid level. The tetraploid *G. dryopteris* ssp. *dryopteris* has a circumboreal distribution and the diploid ssp. *disjunctum* has a more restricted range in Saghalien, southern Kamtchatka, and northwestern North America (Fig. 8). It is suggested that the wide distribution of the species is the result of a recent expansion of a polyploid taxon.

Onoclea sensibilis. The onocleoid ferns are composed of two genera, *Onoclea* and *Matteuccia,* and five species that include a species of putative hybrid origin (Kato & Sahashi, 1980). *Onoclea* consists of two species, *O. sensibilis* and *O. orientalis.* The former is separated into two varieties, var. *sensibilis* of eastern North America and England (probably introduced), and var. *interrupta* of eastern Asia, which differs from var. *sensibilis* in possessing more widely-spaced fertile pinnules (Fig. 9). Paleobotanical evidence shows that in the Cretaceous and Tertiary the *Onoclea sensibilis* group was diversified and distributed more widely than the present, and was known from Alaska, Canada, the United States.

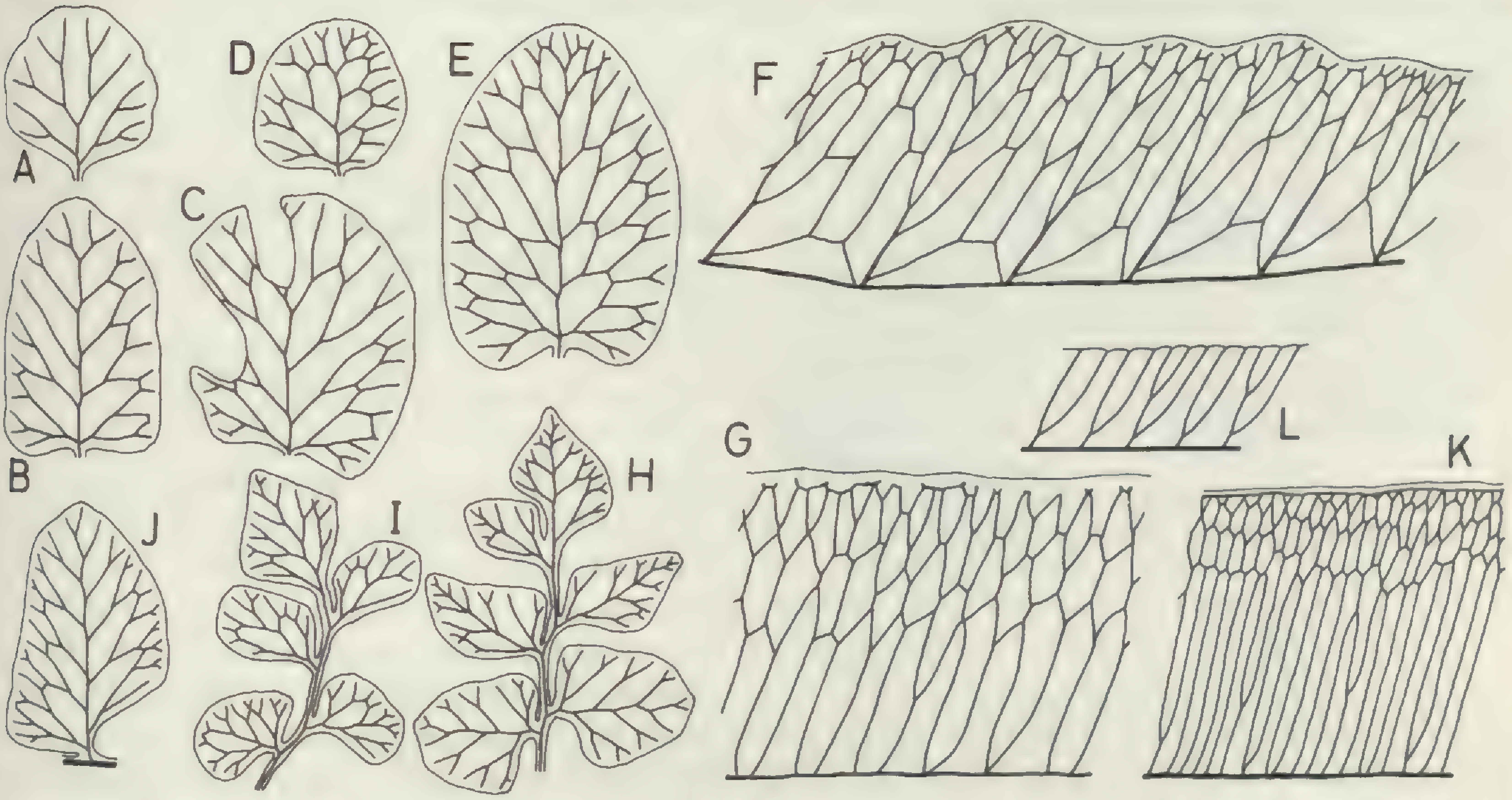

FIGURE 7. Venation of *Diplazium pycnocarpon* and presumably related species.—A–F. *D.* (*Dictyodroma*) *heterophlebium*:—A–E. Juvenile plant.—G–J. *D.* (*Diplaziopsis*) *cavalerianum*:—H–J. Juvenile plants.—K. *D.* (*Hemidictyum*) *marginatum*.—L. *D. pycnocarpon*. A–J, L ×1, K ×½.

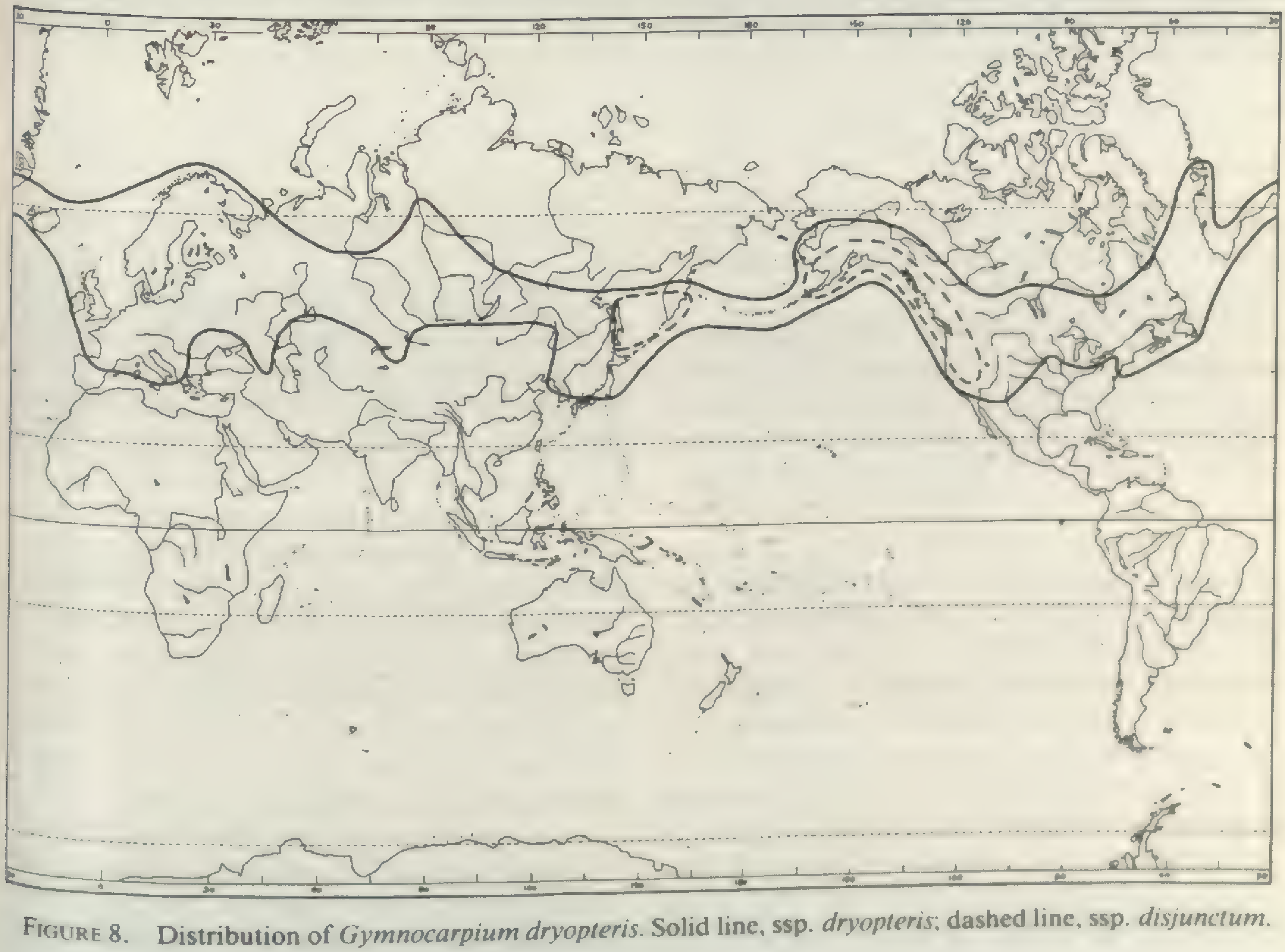

FIGURE 8. Distribution of *Gymnocarpium dryopteris*. Solid line, ssp. *dryopteris*; dashed line, ssp. *disjunctum*.

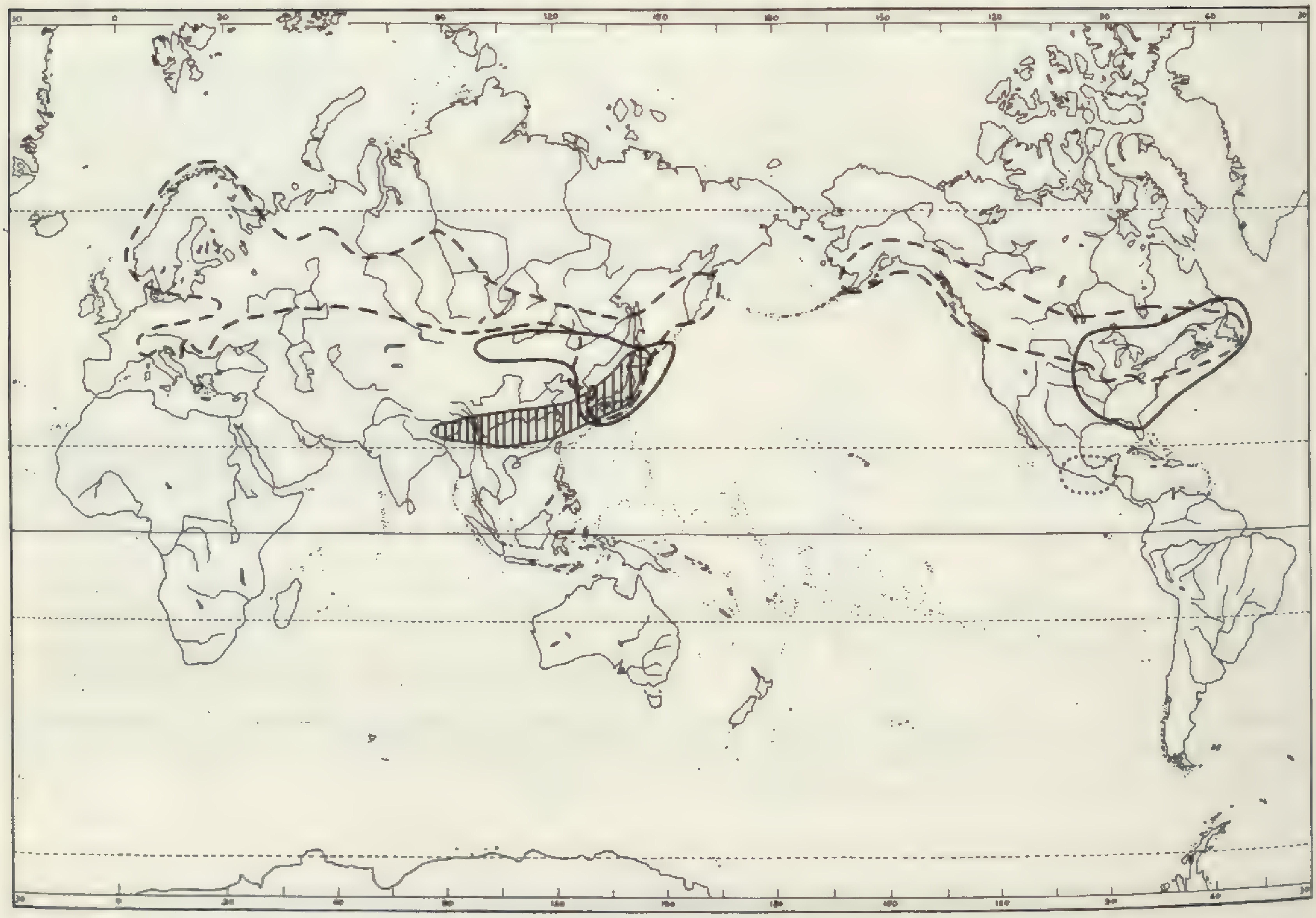

FIGURE 9. Distribution of onocleoid ferns. Solid line, *Onoclea subsibilis*; vertical lines, *O. orientalis*; dotted line, *Matteuccia hintonii*; dashed line, *M. struthiopteris*.

central and southern Europe, and Japan. Most of the fossils are fragments of leaves with reticulate venation, however.

Regarding the taxonomic relationships, Kato and Sahashi (1980) considered that each species of the onocleoid ferns is distinct, *O. sensibilis* and *Matteuccia hintonii* are relatively primitive, and *O. orientalis* and *M. struthiopteris* are derived. Further, that *Onoclea sensibilis* and *Matteuccia hintonii* originated from a common ancestor is suggested by the resemblance in the sagenioid venation of sterile leaves, the compoundly pinnate fertile leaves, and spore ornamentation. From the distribution pattern and presumed taxonomic affinities it is suggested that the onocleoid ferns originated somewhere in Central or North America. *Onoclea orientalis* might have developed in Asia from an *O. sensibilis*-like ancestor whereas *M. struthiopteris* might have originated in North America from a *M. hintonii*-like ancestor and later spread widely in the Northern Hemisphere.

DISCUSSION

From a comparison of the pteridophytes known in the Far East and eastern North America, it is evident that the pteridophyte floras are similar between these two areas, as is the case of the seed plants. It is, however, rather difficult to discuss phytogeographic relationships between any two areas based solely on the present distribution patterns of the extant species. In most cases the distribution of the plants is in good accordance with the geohistory of the areas concerned, and pteridophytes are not exceptional in this respect, despite their easy dispersal by spore. The distribution of pteridophytes is also influenced by environmental factors, especially by such climatic conditions as temperature and moisture, which in turn influence pteridophytes during the entire life cycle from spore germination through sporophyte maturation. Moreover, the distribution of the pteridophytes is strongly dependent upon the vegetation of the areas in which they grow.

The climatic factors influence the vegetation and thus indirectly delimit the distribution. Because the climate in the Far East is more similar to that in eastern North America than to that in western and central North America, at least a part of the geographic similarity of Far East–eastern North American pteridophytes is regulated by such climatic and ecological conditions.

We examined the taxonomic relationships of some apparently identical or vicarious species occurring in temperate North America and Japan, and from these deduced the phytogeographic relationships of each species, although the assumptions are derived from incomplete evidence. The indication is that the apparently identical and vicarious species under consideration have their own phylogenetic background, that the similarity of their present distribution patterns is due to dispersal with allied forests, and that during that time there has been some evolutionary change. Further elucidation of the taxonomic relationships of those species with reference to the morphology, cytology, genetics and ecology surely will contribute to the understanding of the dynamic aspects of the geographic relationships of the fern floras of temperate North America and eastern Asia.

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EASTERN ASIAN–EASTERN NORTH AMERICAN FLORISTIC RELATIONS: THE PLANT COMMUNITY LEVEL

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ABSTRACT

Most comparisons of the temperate floras of eastern North America and eastern Asia have addressed the systematic or floristic level. Data on vegetation pattern and structure, when present, have been broadly descriptive, with little detail on gradient relations or intercommunity pattern. Great Smoky Mountains National Park, the largest eastern temperate preserve of floristic diversity in the United States, lies near the center of development of the North American deciduous forest. The flora of this park was used to model the gradient distributions and ecological characteristics of species with east Asian near-relatives. The disjunct taxa (162 species or 13 percent of the flora) were a highly non-random assortment of the native flora (total = 1,211 species) as a whole: they were more likely to be primitive in phylogenetic standing, perennial, and woody. They were also non-randomly distributed among habitats, being more likely to be found on exclusively terrestrial, forested, and mesic sites. Taxa belonging to genera absent from eastern Asia (232 species or 19 percent of the flora) were an equally interesting non-random sample of the native flora: they were more likely to be herbaceous and advanced in phylogenetic standing. Absent taxa, however, essentially represented a random sample of the flora as a whole in terms of degree of habitat openness and substrate type. When gradient distributions were corrected for overall species richness distributions, absent taxa showed their peak importance on xeric sites. Taxa in wide-ranging north temperate genera (817 species or 67 percent of the flora) generally constituted a random sample of the flora as a whole; they showed peak importance at higher elevations. These data are used to make inferences about the distribution of species richness in the Smokies landscape. Evidence that the eastern Asian temperate deciduous forests were the most diverse temperate forests on earth is also reviewed. Alternative hypotheses concerning the nature of this heightened diversity are discussed.

Investigations of the floristic relationship between temperate eastern Asia and eastern North America generally have treated such relationships at the geographical, systematic, or evolutionary level. There are, however, important ecological correlates to this relationship that have gone, for the most part, untested. This investigation uses a well-known eastern North American landscape, the Great Smoky Mountains, to examine ecological correlates of the floristic relationship. Although others have qualitatively described many of these patterns (cf. Hu, 1936; Cain, 1943; Li, 1952; Wang, 1961), quantitative studies have been lacking. An objective of this research, then, was to develop explicit tests for the distribution of ecological properties in the flora as a function of phytogeography. The landscape distribution of the Great Smoky Mountains flora was used to develop and discuss community level hypotheses on the eastern Asian–North American floristic relationship.

NORTH TEMPERATE DISJUNCTION AND DIVERSITY

The disjunctions between eastern Asia and eastern North American are generally at the generic level, although a few plants are conspecific and others are disjunct only at subfamily or subgeneric levels (Good, 1927; Li, 1952, 1972; Sharp, 1953; Graham, 1972; Wood, 1970, 1972; see also other papers, this volume). About 13 percent of the genera in the southeastern United States is involved (Wood, 1972). Some 62 genera are strictly disjunct; another 58 genera are nearly so, being strongly discontinuous in their range (Wood, 1972; Li, 1952). There are an additional 37 disjunctions at subgeneric and subfamily levels (Li, 1952, 1972; Wood, 1972). These disjunctions probably developed under the combined influence of continental drift, increasing aridity, and climatic cooling during the last 50–75 million years. These events caused fragmentation of the Arcto-Tertiary geoflora, the most diverse remnants of which now dominate the eastern sides of the north temperate continents. Late Cenozoic extinctions were a final factor in the pattern now observed; these were less important in eastern Asia than in eastern North America and less important in the latter area than in other Arcto-Tertiary centers (e.g., Europe and northwestern North America).

The ecological parallels between eastern Asia

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TABLE 1. Diversity ratios for the genera and families of eastern Asian–eastern North American disjunct vascular plants (data calculated from Li, 1952).

Diversity Ratio	n	Eastern Asia	Eastern North America
Genera/family	23	3.6	2.4
Species/genus:			
Temperate genera	37	2.7	1.9
Temperate-tropical genera	19	13.8	3.2
All genera	56	6.5	2.3
Species/family	23	23.4	5.5

and eastern North America have been studied to a lesser extent, but are also intriguing: 1) woody, broad-leaved, deciduous plants are prominent in the disjunct groups and dominate the forested landscapes of both areas (Li, 1952; Wang, 1961; Wood, 1972); 2) disjunct herbaceous taxa tend to be rhizomatous or tuberous, spring-blooming, early-leafing ephemerals or shade-adapted geophytes (Li, 1952); 3) broad-scale generic turnover along environmental gradients is similar in the two areas (for example, both areas have *Quercus-Acer-Betula-Picea* south-to-north latitudinal gradients (Wang, 1961; Braun, 1950); and 4) overall climatic regimes also are similar (e.g., precipitation is available year round). The similarities in life history and physiognomy are presumably the result of descent from common ancestors that has taken place in similar environments (Li, 1972) rather than the result of convergence *because* of similar environments. Nonetheless, these functional parallels have apparently survived some 50 million years of isolation, taxonomic divergence at the specific level, and episodes of worldwide climatic change. Li (1952) also noted phylogenetic correlates to the disjunctions: Ranalian families are prominent in the list of disjunct groups.

By far the most important observation at the community level is the comparative species richness of the various remnants of the Arcto-Tertiary flora. Most of the disjunct genera have more species in eastern Asia than in eastern North America (Li, 1952; Table 1). In addition, the families with disjunct genera in both areas often have more total genera in eastern Asia than in eastern North America. The result is that there are over four times as many species in the disjunct groups in eastern Asia (Table 1). In addition, temperate Asian families and genera that presently are not native in eastern North America are known from the fossil record there (notably *Ginkgo, Metasequoia, Cercidiphyllum, Dipteronia, Pterocarya,* and *Zelkova*; Axelrod, 1984). These same statements apply to the contrast between eastern North America and Europe: North America is richer in deciduous forest taxa than is Europe and some of the presently disjunct American-Asian taxa are known as fossils in Europe (Wood 1970; Axelrod, 1984). The differences in floristic richness among eastern Asia, North America, and Europe probably results from differing Pleistocene extinction rates in the three areas. Prior to the advent of man, eastern Asia harbored the world's most diverse temperate forests.

We should be cautious in accepting this apparently higher species richness in eastern Asia, however. Although disjunct groups are more diverse in eastern Asia, other non-disjunct groups can be richer in North America (for example, this seems to be true in Asteraceae). Communities from the two continents must be carefully compared. For example, Wang (1961) used the term "mixed mesophytic" forest in China for the rich mixed evergreen-deciduous forests of southerly latitudes. The "mixed-mesophytic" forest of eastern North America is almost entirely deciduous (Braun, 1950). Further, eastern Asia has a much more complete and complex temperate to tropical gradient on mesic sites (this is a gradient of increasing species richness); the gradient in eastern North America is interrupted by the coastal plain and Gulf of Mexico. Finally, there might also be differences in taxonomic treatment in the two areas. Despite these caveats, some of the increased richness in eastern Asia is hardly debatable (e.g., the striped-bark maples, *Acer* sect. *Macrantha* or the distinctive endemic Asian genera already noted).

If the heightened species richness is real, its resolution is fundamental to community level comparisons between eastern Asia and eastern North America. How is the added species richness partitioned in the landscape? There are three possibilities (Whittaker, 1972): 1) higher alpha diversity (within-community species packing or point diversity); 2) higher beta diversity (closer species packing along gradients); and 3) higher gamma diversity (closer species packing across whole landscapes). Three kinds of gamma diversity are: a) that caused by different habitat diversities within one landscape; b) that caused by the interplay of natural disturbance and

succession (White, 1979); and c) that caused by geographic isolation and allopatric speciation (i.e., the development of sibling species across geographic barriers).

At present, a complete resolution of these questions is impossible: quantitative data on Chinese forests are scarce. There is some question whether a resolution will ever be possible: that country has been under intense pressures of population growth for centuries (Smil, 1981) and has only recently formulated conservation policies (Wang, 1980).

This paper, then, addresses these questions through an analysis of one relatively well-known eastern North American landscape, the Great Smoky Mountains, in North Carolina and Tennessee, which lies near the center of diversity of the eastern deciduous forest (Braun, 1950; Whittaker, 1956; Monk, 1967). I examined the community level using two aspects of the flora of this region: autecology (how the plants behave—their life history, growth form, gradient distribution), and synecology (here, the diversity patterns of the plant communities). Ecological properties of the flora were modelled as a function of phytogeographical category. Primary questions were: Are the disjunct taxa a random assortment of the life histories and growth forms of the flora as a whole? Are the disjunct taxa randomly distributed in the Smokies landscape? How is species richness distributed in the landscape? Although many of the questions had been qualitatively addressed previously (see Li, 1952; Cain, 1943), they previously had not been tested explicitly against appropriate random models.

The Study Area: The Great Smoky Mountains

Great Smoky Mountains National Park (hereafter, GRSM: 208,000 ha) is the largest United States National Park in a deciduous forest landscape. It is located at 35°30′N latitude in the southern Appalachian Mountains (Fig. 1), near the richest part of the deciduous forest (Braun, 1950; Monk, 1967). Elevation ranges from 260 to 2,021 m. The climate is continental: July temperature averages 22°C at 445 m and 13.5°C at 1,920 m; January temperature averages 4.5°C at 445 m and −0.8°C at 1,920 m (Shanks, 1954). Precipitation averages 147 cm at 445 m and 231 cm at 1,920 m. Deciduous forest is dominant on mesic to subxeric sites below 1,900 m. Spruce-fir evergreen needle-leaved forest is dominant above this elevation. Pine forest dominates the driest sites at low and mid elevations and hemlock dominates cool stream valleys (Whittaker, 1956). The mountains are not high enough for a climatic tree line, but two kinds of tree-less communities (grassy balds and heath balds) occur; these are probably a result of disturbance and/or exposure.

Methods

The 1,211 native vascular plants of Great Smoky Mountains National Park (White, 1982) are divided into three phytogeographical categories (this is usually done at the generic level—see Wood, 1972): 1) taxa strictly disjunct (e.g., *Caulophyllum*) or strongly discontinuous (e.g., *Aesculus*), found in eastern Asia, eastern North America, and occasionally in one or two other Arcto-Tertiary refuges (e.g., Pacific northwestern North America and mountainous southeastern Europe); 2) genera widely distributed in the North Temperate zone (e.g., *Quercus*); and 3) North American genera absent from eastern Asia (e.g., *Phacelia*). There is continuous gradation from disjunct to discontinuous to wide-ranging genera; for disjunct taxa, the floristic judgments of Wood (1970, 1972) and Li (1952, 1972) are followed.

All plants were coded for a series of autecological characteristics: life history, growth form, deciduousness, height when mature, life form (Raunkiaer, 1934), and phenology. Community data developed through a vegetation monitoring program and distribution data organized through computerization of herbarium labels were used to code presence of the plant species along three dominant environmental gradients: 1) elevation, 2) site moisture class (hydric, mesic, submesic-subxeric, xeric), and 3) relationship to disturbance and succession (habitat coded as: full sun, partial shade, and full shade). These three gradients are strongly correlated with plant distribution in the southern Appalachians (Whittaker, 1956; Golden, 1974).

Species richness within communites (alpha diversity) and along gradients (beta diversity) was derived from the distributional data described above. These data were also used for gauging the effect of disturbance patches on species richness. Landscape (gamma) diversity was approached using an analysis of plant abundance and distribution; all species were coded for abundance and evenness of distribution throughout the park

FIGURE 1. Location of Great Smoky Mountains National Park, North Carolina and Tennessee.

(both taken from White, 1982). Only species richness was analyzed; dominance relations of species within communities were not addressed.

Finally, a phylogenetic code was developed to test the distribution of taxa by presumed distance from the Ranales. Higher groups were assigned to three categories (Stebbins, 1974): 1) Primitive—Superorders Magnoliidae and Alismatidae; 2) Intermediate—Superorders Rosidae, Hamamelidae, Dilleniidae, and Caryophyllidae, and Orders Liliales, Commelinales, and Juncales; and 3) Advanced—Superorder Asteridae, and Orders Orchidales, Cyperales, and Poales.

Plants in the three phytogeographical categories were contrasted with the total native flora for each of the phylogenetic, natural history, and habitat variables. The null hypothesis in each case was that the plants in the separate geographical categories represented a random sample of the flora as a whole; the probability level of 0.05 was used as the criterion of significance. The data were analyzed in two ways: 1) percent distribution of ecological attributes within phytogeographical categories (i.e., normalizing to a common species pool, 100 taxa, within each category); and 2) percent distribution of phytogeographical categories within each ecological characteristic (i.e., percent contribution of each floristic category to a particular ecological category. In the former case, the spectrum of ecological characteristics within a phytogeographical category was compared to that spectrum in the flora as a whole; in the latter case, the percent contribution of the floristic category to a particular ecological category was compared to its percent contribution to the flora as a whole. Statistical analysis and graphic presentation were done at the University of Tennessee Computing Center.

RESULTS

Thirteen percent of GRSM's native vascular plants belong to genera that are disjunct or discontinuous (hereafter called "disjunct" plants); 19 percent belong to genera that are absent from eastern Asia (hereafter "absent" plants); and 68 percent belong to genera with wide north temperate distributions (hereafter "no. temperate" plants) (Table 2). Because the latter group of plants also occurs in eastern Asia, 81 percent of the GRSM flora belong to genera that occur in eastern Asia. Twenty-five percent of GRSM genera are in the disjunct category; these genera account for about 60 percent of the disjunct genera of Wood (1972). The disjunct genera are poorer (average = 1.5) in species than the total native genera (average = 2.8) (Table 2). The absent genera (average = 1.9) also are relatively species-poor, whereas the widely distributed north temperate genera are relatively species-rich (average = 3.5). The disjunct taxa have a lower species/genus ratio than that extracted from Li (1952) for all of eastern North America (average = 1.9 species/genus, Table 1).

Phylogeny. The distribution of taxa in the phylogenetic categories is highly non-random (Table 3). Disjunct taxa are three times more likely to be "Ranalian" than the total native flora; disjunct taxa contribute 47 percent of all native taxa in this category, although they account for only 13 percent of the flora as a whole. By contrast, only one percent of absent taxa are "Ranalian," whereas 65 percent (the highest of any of the groups) are in the third, most advanced, phylogenetic category. Disjunct taxa are strongly under-represented in the latter category (14 percent of phytogeographic disjuncts are category 3; four percent of all phylogenetic disjunct plants are in category 3). As might be expected, then, Poaceae (Koyama & Kawano, 1964) and Asteraceae are relatively poor in disjunct taxa, but relatively rich in taxa in the absent category (Table 3). Taxa in widely distributed north temperate genera are generally a random selection of the flora as a whole; the only significant departure from a random model is an under-representation in the "Ranalian" phylogenetic category.

AUTECOLOGY

Life history. The disjunct taxa are more strongly perennial (98 percent of all disjuncts) and woody (51 percent of all disjuncts), than the flora as a whole (Table 4). Ninety-nine percent of the annual and 91 percent of the biennial plants are contributed by the non-disjunct phytogeographic categories. The absent taxa are strongly herbaceous (92 percent); except for woodiness, however, these taxa are essentially random samples of the flora as a whole. North temperate taxa are over-represented in the herbaceous category and under-represented in the woody category, but otherwise also are randomly distributed compared to the flora as a whole. Interestingly, the disjunct taxa have a significantly higher percentage of evergreens (eight percent), despite the common observation that disjuncts are associated with deciduous forest landscape.

Growth form and mature height. Disjunct

TABLE 2. Phytogeographical categories in the native flora of Great Smoky Mountains National Park (the distribution of the genera does not sum to 100 percent because of taxa that are disjunct at other than the generic level).

	Taxa (n)	%	Genera (n)	%	Species/ Genus
Absent	232	19	125	29	1.9
Disjunct	162	13	108	25	1.5
North temperate	817	68	231	53	3.5
Native flora	1,211	100	437	100	2.8

taxa are dominantly phanerophytes (42 percent) and geophytes (33 percent); these percentages are higher in the disjunct category than in any other phytogeographic category (Table 5). By contrast, taxa belonging to genera absent from eastern Asia are dominantly hemicryptophytes (54 percent) and have a relatively low percentage of phanerophytes (seven percent). The absent taxa are over-represented in therophytes (25 percent) and geophytes (25 percent), whereas the disjunct taxa are over-represented in the phanerophyte (33 percent), chamaephyte (40 percent), and geophyte categories (23 percent).

Disjunct taxa have a higher percentage distribution in the taller height classes (34 percent of all disjunct taxa reach at least 4 m in height; 55 percent of all plants surpassing 4 m in height are disjunct taxa) than any other floristic category (Table 5). Most taxa absent from eastern Asia are in the smaller height classes (95 percent reach less than 2 m tall), and this phytogeographical category makes its strongest contribution to the flora in the smaller sizes (Table 5).

Phenology and flower color. Seventy-two percent of the disjunct taxa bloom in spring and less than one percent in autumn (Table 6). The peak flowering time for absent taxa is summer (58 percent). Percent contribution to the phenologic periods also reflects this: disjunct taxa make their strongest contribution to the spring flora (22 percent), whereas absent taxa make their peak contribution to the aestival flora (29 percent). Flower color is also skewed: the most important color for disjunct taxa is white (44 percent of all disjunct taxa). White is also the most important flower color for absent taxa (28 percent), but that group has the highest percentage yellow (23 percent) and blue-purple (19 percent) flowers of any floristic category and makes a relatively strong total contribution to those categories (30 percent of all yellow and 34 percent of all blue-purple flowered taxa are absent from eastern Asia—the yellow-flowered taxa occur mostly in the Asteraceae, a family poor in disjunct taxa, as noted above).

Disjunct taxa also have a significantly ($P <$

TABLE 3. Distribution of taxa in phylogenetic and phytogeographical categories (see text for an explanation of the groups). The random model in Part A below is percentage of native taxa in the phylogenetic category; in Part B it is the percentage of the phytogeographic category in the flora as a whole. ** = $P < 0.01$; $^{+}$ = $P < 0.001$; $^{++}$ = $P < 0.0001$; ns = not significant at the 0.05 level.

Phytogeographic Category	Total Taxa (n)	% Native Flora	Phylogenetic Categories 1 n = 62	2 n = 534	3 n = 545	Poaceae n = 92	Asteraceae n = 138
A. Distribution within phytogeographic categories:							
Absent	232		1^{+}	34^{**}	65^{++}	9 ns	20^{++}
Disjunct	162		19^{++}	67^{++}	14^{++}	2^{**}	2^{++}
North temperate	817		5 ns	47 ns	48 ns	8 ns	11 ns
Native flora	1,211		6	46	48	8	11
B. Distribution within phylogenetic categories:							
Absent		19	3^{++}	15^{**}	28^{**}	22 ns	34^{++}
Disjunct		13	47^{++}	20^{+}	4^{++}	3^{**}	2^{++}
North temperate		68	50^{+}	65 ns	68 ns	75 ns	64 ns

TABLE 4. Distribution of taxa in life history and phytogeographic categories (see text for an explanation of the latter). The random model in Part A below is the percentage of native taxa in the life history categories; in Part B it is the percentage of the phytogeographic category in the flora as a whole. * = $P < 0.05$; ** = $P < 0.01$; $^{+}$ = $P < 0.001$; $^{++}$ = $P < 0.0001$; ns = not significant at the 0.05 level.

Phytogeographic Category	Total Taxa (n)	% Native Flora	Life History: Perenn. n = 1,045	Life History: Annual n = 131	Life History: Bienn. n = 35	Woodiness: Woody n = 246	Woodiness: Herbac. n = 965	Deciduousness: Decid. n = 1,137	Deciduousness: Evergreen n = 74
A. Distribution within phytogeographic categories:									
Absent	232		83 ns	14 ns	3 ns	8^{++}	92^{++}	96 ns	4 ns
Disjunct	162		98^{++}	1^{++}	1^{++}	51^{++}	49^{++}	92 ns	8*
North temperate	817		85 ns	12 ns	3 ns	28 ns	82 ns	94 ns	6 ns
Native flora	1,211		86	11	3	20	80	94	6
B. Distribution by life history:									
Absent		19	18 ns	25*	20 ns	7^{++}	22^{++}	20 ns	12 ns
Disjunct		13	15*	1^{++}	9 ns	33^{++}	8^{++}	13 ns	20 ns
North temperate		68	67 ns	74 ns	71 ns	60*	70*	67 ns	68 ns

TABLE 5. Distribution by growth form and phytogeographic category (see text for an explanation of the latter). The random model in Part A below is the percentage of native taxa in the life history categories; in Part B it is the percentage of the phytogeographic category in the flora as a whole. * = $P < 0.05$; ** = $P < 0.01$; $^{+}$ = $P < 0.001$; $^{++}$ = $P < 0.0001$; ns = not significant at the 0.05 level.

Phytogeographic Category	Total Taxa (n)	% Native Flora	Raunkiaer Class: Phaner. n = 235	Raunkiaer Class: Chamae. n = 10	Raunkiaer Class: Hemi-crypt. n = 605	Raunkiaer Class: Geo. n = 229	Raunkiaer Class: Thero. n = 132	Height when Mature (m): <1 n = 799	Height when Mature (m): 1–2 n = 212	Height when Mature (m): 2–4 n = 76	Height when Mature (m): 4–8 n = 21	Height when Mature (m): >8 n = 103
A. Distribution within phytogeographic categories:												
Absent	232		7^{++}	0.4 ns	54 ns	24*	14 ns	72^{++}	23*	3*	0.4**	1^{++}
Disjunct	162		47^{++}	3 ns	16^{++}	33^{+}	11^{++}	44^{++}	9^{++}	12**	9^{++}	25^{++}
North temperate	817		17 ns	0.6 ns	56**	15**	12 ns	69 ns	18 ns	6 ns	0.6**	7*
Native flora	1,211		19	0.8	50	19	11	66	17	6	2	9
B. Distribution by growth form:												
Absent		19	7^{++}	10 ns	21 ns	25*	25*	20 ns	25*	9**	5*	3^{++}
Disjunct		13	33^{++}	40*	4^{++}	23^{++}	2^{++}	9^{+}	7^{+}	26**	71^{++}	39^{++}
North temperate		68	60*	50 ns	75^{++}	52^{++}	73 ns	71*	68 ns	65 ns	27^{++}	58*

TABLE 6. *Distribution by phenology, flower color, and phytogeographic category (percentages by phenology do not sum to 100 because some plants bloom throughout the year). The random model in Part A below is the percentage of native taxa by floral categories; in Part B it is the percentage of the phytogeographic category in the flora as a whole.* * = < 0.05; ** = $P < 0.01$; $^{+}$ = $P < 0.001$; $^{++}$ = $P < 0.0001$; ns = not significant at the 0.05 level.

Phytogeographic Category	Total Taxa (n)	% Native Flora	Phenology: Vernal n = 79	Late Vernal n = 562	Aest. n = 467	Autumn. n = 77	Flower Color: Brown n = 21	Green n = 343	Blue-purple n = 130	Pink-Red n = 91	Orange n = 13	Yellow n = 178	White n = 365
A. Distribution within phytogeographic categories:													
Absent	232		4**	33^{++}	58^{++}	4 ns	2 ns	15^{++}	19^{++}	11 ns	2 ns	23**	28 ns
Disjunct	162		14^{++}	58**	27^{+}	0.6**	7^{++}	27 ns	4**	9 ns	0.7 ns	9**	44^{+}
North temperate	817		6 ns	48 ns	35**	8**	6**	36^{++}	11 ns	7 ns	1 ns	15 ns	31*
Native flora	1,211		7	46	39	6	2	30	11	8	1	16	32
B. Distribution by floral characteristics:													
Absent		19	13 ns	13^{++}	29^{++}	13 ns	24 ns	10^{++}	34^{++}	28**	31 ns	30^{++}	18 ns
Disjunct		13	28^{++}	16*	9**	1^{+}	52^{++}	13 ns	5**	14 ns	8 ns	8**	19**
North temperate		68	59*	71 ns	62**	86^{+}	24^{++}	77^{++}	61*	58*	61 ns	62 ns	63*

TABLE 7. Distribution by habitat and phytogeographic categories (see text for an explanation of the latter). The random model in Part A below is the percentage of native taxa in the life history categories; in Part B it is the percentage of the phytogeographic category in the flora as a whole. * = $P < 0.05$; ** = $P < 0.01$; $^{++}$ = $P < 0.0001$; ns = not significant at the 0.05 level.

Phytogeographic Categories	Total Taxa (n)	% Native Flora	Habitat (Substrate) Categories: Terrestrial n = 932	Wetlands n = 230	Rock Outcrops n = 36	Epiphytic n = 13	Habitat Openness: Forest n = 488	Intermed. n = 396	Open n = 327
A. Distribution by phytogeography:									
Absent	232		82*	14*	3 ns	0.4 ns	41 ns	34 ns	25 ns
Disjunct	162		91^{++}	8^{++}	1*	0 ns	66^{++}	28 ns	6^{++}
North temperate	817		73**	22*	4 ns	1*	35 ns	33 ns	32*
Native flora	1,211		77	19	3	0.5	40	33	27
B. Distribution by habitat:									
Absent		19	20 ns	14*	19 ns	7 ns	19 ns	20 ns	17 ns
Disjunct		13	15*	5^{++}	4*	0*	22^{++}	12 ns	3^{++}
North temperate		68	65*	81^{++}	77^{++}	93 ns	59^{++}	68 ns	80^{++}

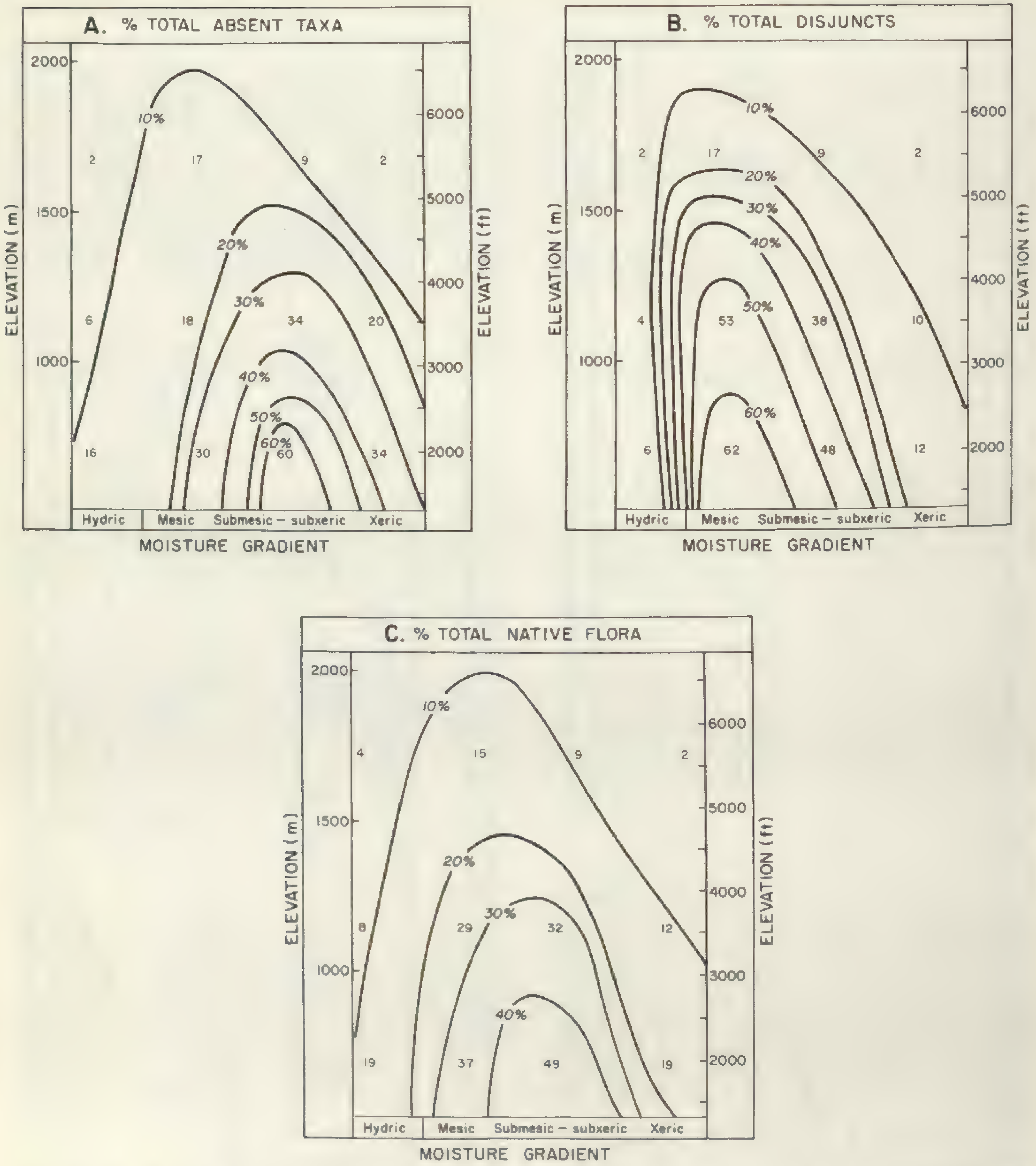

FIGURE 2. Percent distribution of GRSM species along a two-dimensional environmental field. Contours are generalized by ten percent classes; representative data are cited for low, mid, and high elevations and for hydric (wetland), mesic, submesic-subxeric, and xeric sites. A. Absent taxa (232 taxa). B. Disjuncts (162 taxa). C. Total native flora (1,211 taxa).

0.001) earlier peak leaf period (13 percent of all disjuncts and 31 percent of all disjunct herbs have peak leaf periods in spring) than either the absent (eight percent of all taxa, 25 percent of herbaceous taxa have peak leaf periods in spring) or north temperate groups (seven percent of all taxa, 15 percent of herbaceous taxa have peak leaf periods in spring). However, for all phytogeographical categories the peak leaf period is dominantly summer (no significant differences from the total native flora value of 85 percent are found).

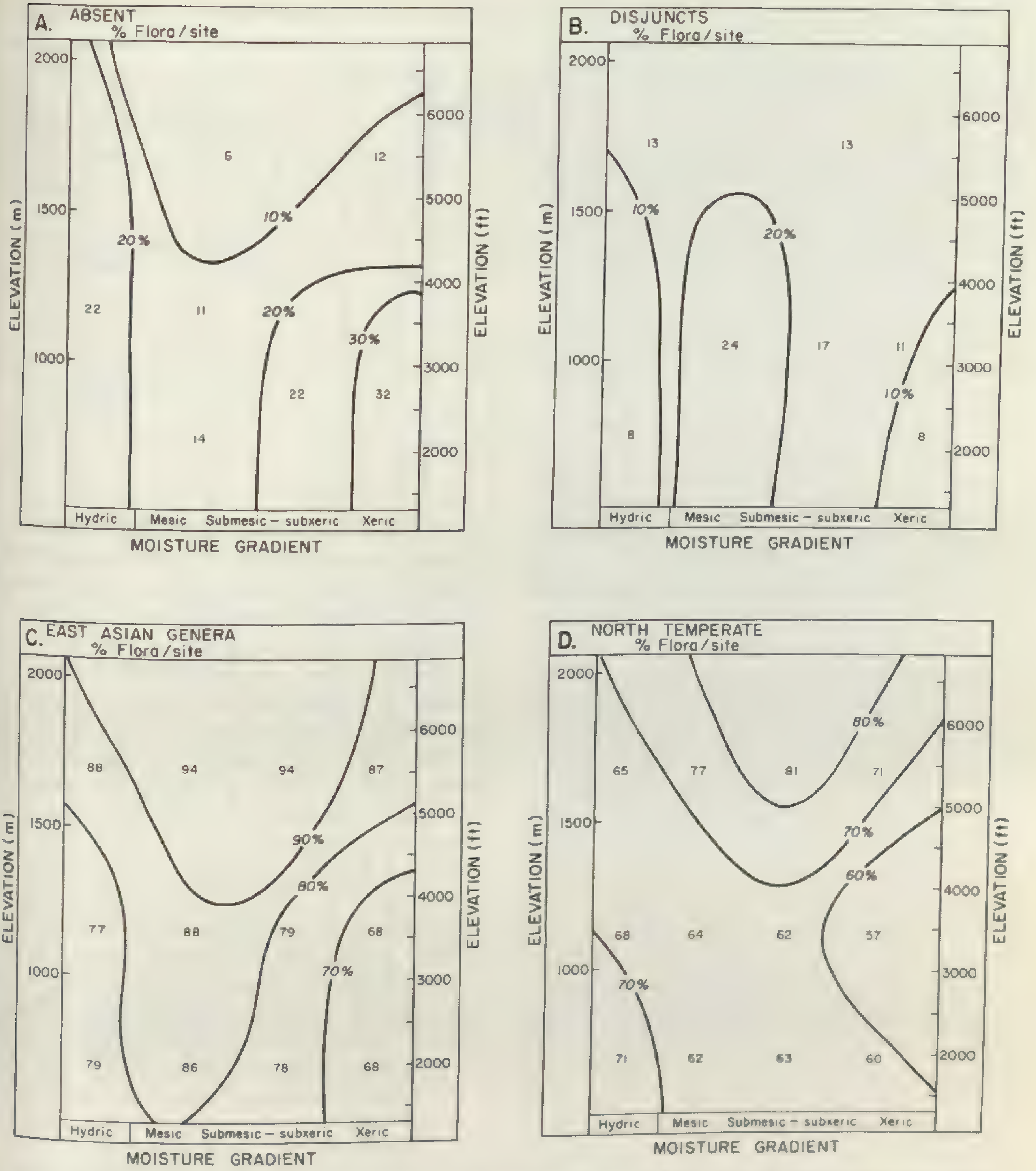

FIGURE 3. Percent contribution of GRSM species to the total expected flora as a function of site. Contours are generalized by ten percent classes; representative data are for low, mid, and high elevations, and for hydric (wetland), mesic, submesic-subxeric, and xeric sites. These diagrams correct for the general decrease of species richness as seen in Figure 2A. A. Absent taxa (232 taxa). B. Disjuncts (162 taxa). C. North temperate taxa (817 taxa). D. All East Asian genera (979 taxa). Only forested sites are shown (see text).

SYNECOLOGY: HABITATS AND GRADIENT DISTRIBUTIONS

Habitat. The disjunct taxa are predominantly plants of terrestrial (91 percent of all disjuncts) and forested (66 percent of all disjuncts) habitats. In both cases this is a significant departure from a random distribution (Table 7). Absent taxa are also over-represented in terrestrial habitats, but are otherwise more or less a random sample of the flora as a whole. Plants of open and wetland habitats dominantly belong to wide-ranging north temperate genera. Despite the fact that the GRSM landscape is heavily forested (99 percent), 27 per-

cent of the park's native plants are found only in open, non-forested habitats (Table 7). Disjunct taxa are strongly under-represented in these open habitats.

Distribution on environmental gradients. Both absent taxa and disjunct taxa have distribution peaks at low elevations (Fig. 2A–B). The disjunct taxa, however, are displaced toward mesic site classes, whereas the absent taxa peak on submesic to subxeric sites. Absent taxa are more strongly represented at the hydric and xeric extremes (16 and 34 percent, respectively of all absent taxa), whereas numbers of disjunct taxa decline more strongly away from the mesic site class. For both phytogeographical categories, however, the total percent decline with elevation is similar—from about 60 percent of the total in the floristic group to about two percent from low to high elevations (Fig. 2A–B). These trends parallel the diversity patterns of the native flora as a whole (Fig. 2C), but here the diversity decline is somewhat less steep (it declines from 50 to two percent with elevation). The distribution of the total native flora is similar to that of the absent taxa, in that there is a submesic-subxeric peak at low elevations and a gradual decline toward moisture extremes.

Two simplifications are possible to better contrast the three floristic groups in terms of landscape distribution. First, because disjunct taxa are unimportant on open sites (*Liriodendron* is an interesting exception), the data base was reduced to plants of forested sites only. Second, because the overall species richness gradient parallels that of the separate phytogeographic groups (Fig. 2A–C), the data were expressed as a percent contribution to the total flora expected on a given site (Fig. 3A–D). In this manner, most of the information on disjuncts available in the 3-dimensional array (elevation, site moisture, habitat openness) is portrayed in two dimensions.

When the data are expressed in this way, the absent taxa show a peak importance in xeric sites, a secondary peak in hydric sites, and a trough in mesic sites (Fig. 3A). Disjuncts show a very different distribution–their peak importance is on mesic sites (Fig. 3B). Taxa of wide-ranging north temperate genera show yet a third pattern, with peak importance at high elevations (the only group to show such an increase with elevation; Fig. 3C). The north temperate taxa are least important on xeric low- to mid-elevation sites; these taxa have a secondary peak on hydric sites.

TABLE 8. Rarity and distribution of taxa in the GRSM flora (from White, 1982). Plants found "throughout" the park are not geographically restricted in the park as a whole. The random model assumes distribution in rarity or distribution categories as a function of the total native flora. * = $P < 0.05$; ** = $P < 0.01$; + = $P < 0.001$; ++ = $P < 0.0001$; ns = not significant at the 0.05 level.

Phytogeographical Category	Total Taxa (n)	Rarity				Throughout	Single Habitat Class Records		
		Park Rare	Total of Scarce, Rare & Very Rare	Infrequent–Occasional	Frequent–Common		Elevation	Site Moisture	Openness
Absent	232	18 ns	32 ns	40^{++}	28^{+}	59 ns	50 ns	57 ns	66 ns
Disjunct	162	15 ns	24**	14^{++}	62^{++}	75*	57^{+}	53*	72*
North temperate	817	14 ns	37 ns	28 ns	35 ns	60 ns	53 ns	62 ns	67 ns
Native flora	1,211	15	34	27	37	62	50	60	67

TABLE 9. Narrowly distributed and widely distributed species and an index of beta diversity for two broad-scale gradients.

Phytogeographical Category	Narrowly Restricted Species	Widely Distributed Species	Species Turnover Ratio
A. Elevation gradient:			
Absent	115	127	0.9
Disjunct	60	102	0.6
North temperate	429	388	1.1
Native flora	604	607	1.0
B. Site moisture classes:			
Absent	133	95	1.4
Disjunct	86	76	1.1
North temperate	505	312	1.6
Native flora	724	487	1.5

Disjunct taxa and taxa of wide-ranging genera both occur in eastern Asia. The importance of these two groups is summed in Figure 3D, which shows the percent of forest flora belonging to genera common to eastern Asia as a function of elevation and site moisture class. Eastern Asian genera have their peak distribution on high elevation mesic sites and decline in importance with decreasing elevation and toward extreme site moisture classes. Xeric sites have the lowest importance in distribution of eastern Asian genera. Overall, 85 to 95 percent of the taxa on mesic sites belong to genera that also occur in eastern Asia.

If life history and environmental distribution are combined, these patterns are reinforced. Forty-two percent of all woody taxa on mesic low- to mid-elevation forested sites belong to disjunct genera; 95 percent of all woody plants on mesic low- to mid-elevation forested sites belong to genera that also occur in eastern Asia.

RARITY AND PARK DISTRIBUTION

The phytogeographic categories were contrasted in rarity and park distribution in order to gauge the effect of sporadic distributions on the richness gradients as a whole (Table 8). Disjunct taxa have a lower percent rarity, both in terms of the rarest elements of the park flora and the sum of very rare, rare, and scarce plants. Disjunct taxa are over-represented among frequent and common plants. Disjunct plants are also well-distributed throughout the Smokies (75 percent of all disjuncts are found throughout the park, the highest percent of any of the phytogeographic groups). The absent taxa are generally a random sample of the flora as a whole, but intermediately common taxa are over-represented and common taxa are under-represented.

Another aspect of distribution breadth was also analyzed: the phytogeographical categories were contrasted in the percentage of taxa restricted to single habitat classes along the three dominant environmental gradients. Two of these gradients were already coded as broad habitat classes: site moisture class (hydric, mesic, submesic-subxeric, xeric) and habitat openness (forested, intermediate, open). Elevation data were summarized in three belts: low (260–760 m; 850–2,500 ft), mid (760–1,370 m; 2,500–4,500 ft), and high (1,370–2,021 m; 4,500–6,621 ft). The results show that disjunct taxa are narrowly distributed along only one of the gradients: habitat openness (Table 8), as noted earlier. In other ways (elevation, site moisture class), the disjunct taxa are less restricted to habitat classes than would be expected based upon chance alone. The other phytogeographical categories are essentially random samples of the flora as a whole in terms of habitat restrictions (Table 8).

The data on gradient restrictions were also used for an index of gradient (beta) diversity. The number of species replacements between the habitat classes (the number of new restricted species encountered in each habitat class) was compared to the number of widely distributed taxa (Table 9). The north temperate taxa have the highest species turnover ratio, whereas the disjunct taxa have the lowest. All phytogeographic categories have higher turnover ratios for

the site moisture class gradient compared to the elevation gradient.

DISCUSSION

Taxa belonging to disjunct genera in GRSM are clearly a non-random sample of the native flora: they are much more likely to be perennial, woody, primitive or intermediate in phylogenetic terms, and earlier in blooming and leafing. Disjunct herbaceous taxa are more likely to be geophytes than are non-disjunct taxa. The taxa belonging to disjunct genera are also non-randomly distributed among habitats—they are more likely to be found on terrestrial, forested, and mesic sites than are non-disjunct taxa. Disjunct taxa are generally more common and more widely distributed in the park than their non-disjunct counterparts.

Unexpectedly, taxa belonging to genera absent from eastern Asia proved just as interesting as the disjunct taxa. For many attributes they also are a non-random assortment of the flora as a whole: absent taxa are more advanced in phylogenetic standing, more herbaceous, less apt to be phanerophytes, shorter in mature height, later blooming (with a stronger representation of yellow flowers), and later leafing. Absent taxa are, however, essentially a random sample of the flora as a whole with regard to substrate and habitat openness. Absent taxa also parallel the whole native flora in gradient distribution: they show a peak occurrence in low elevation submesic-subxeric sites. When the gradient patterns are corrected for the overall distribution of species richness, absent taxa have their peak importance on xeric sites where they make up 20–35 percent of the flora. McVaugh (1943) found that xeric site species (on southeastern United States granite outcrops) had strong phytogeographical ties to western North America. Although the xeric sites analyzed in GRSM are dominated by pine forests, rather than open outcrop communities, the pattern is similar. The taxa of genera absent from eastern Asia are often ones with southwestern United States relatives.

These facts support earlier observations on prominent features of the disjunct taxa: their woodiness (Li, 1952; Wood, 1972), primitiveness (Li, 1952; Sharp, 1953), and habitat distribution (Cain, 1943). Further, there is a clear relationship between life history traits and habitat. Early leafing, geophytic, herbaceous plants are adapted to mesic deciduous forests; in this way the disjunct taxa parallel the gradient distribution of life history traits in the Southern Appalachians as a whole (Thomas Givnish, pers. comm.). The importance of large phanerophytes is also related to habitat: mesic, low- to mid-elevation forests have the largest biomass of any GRSM communities. The importance of phanerophytes in favorable environments is one of the broad-scale generalizations of the geography of life forms.

Several inferences concerning the contribution of disjunct taxa to the pattern of species richness in the GRSM landscape can be made from these data. Disjunct taxa do not contribute to the several kinds of gamma (whole landscape) diversity. Disjunct taxa are unimportant in open, disturbance-produced habitats. They are relatively frequent plants with uniform distributions throughout the park. They do not increase GRSM richness through occurrence in rare habitats; neither are they rare in common habitats. As a component of the flora, they make no disproportionate contribution to landscape richness per se: they are not patchily distributed.

Disjunct taxa are also relatively unimportant in their contribution to species turnover along gradients (beta diversity). Disjunct taxa decrease more sharply in richness along gradients than the flora as a whole. They do not disproportionately increase richness on extreme moisture class sites or at high elevations (where total diversity is relatively low). Individual taxa are not more narrowly distributed on gradients than non-disjunct taxa, except for habitat openness. The strong inference is that disjunct taxa do not have a higher turnover of taxa along gradients than the flora as a whole, and do not contribute disproportionately to beta diversity.

The disjunct plants are, however, concentrated in mesic low- to mid-elevation forests. These are relatively species-rich habitats for the GRSM landscape as a whole. The contribution of disjunct plants to species richness, then, is non-random in the landscape: from the data presented here, the inference is that this contribution is to alpha (within community) richness. It was, in fact, the concentration of Arcto-Tertiary plants in mesic low- to mid-elevation forests that led Cain (1943) to infer 60 million years of stasis in Southern Appalachian vegetation (since refuted, Delcourt & Delcourt, 1979, 1981). One can summarize the Smokies pattern: disjunct taxa increase the richness of communities that are relatively rich in non-disjunct taxa. This contri-

bution is habitat concentrated, rather than diffused across the landscape or along gradients.

These conclusions only can be extended beyond the study area with caution, however. Only 60 percent of Wood's (1972) disjunct or discontinuous genera occur in GRSM. For all disjunct genera, Li (1952) reported a higher species/genus ratio than that reported here. This is true for North American species of these genera (1.9 species/genus vs. 1.5 for the Smokies) as well as for eastern Asian species, as discussed earlier. Thus, there are, on the continental scale, additional genera and species in eastern North America not accounted for by the GRSM model of species richness. Finally, if the eastern Asian flora was less affected by Pleistocene changes than that of eastern North America (Delcourt & Delcourt, 1979, 1981), there are implications for distribution of species richness. Less environmental change might leave ecological barriers to migration intact and might pose less of a threat to rare, patchily distributed species. These questions will be resolved only as quantitative data become available from the temperate deciduous forests of eastern China, the richest such forests on earth.

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ISOENZYME VERIFICATION OF AMERICAN-CHINESE HYBRIDS OF *LIQUIDAMBAR* AND *LIRIODENDRON*[1]

SHAN-AN HE[2] AND FRANK S. SANTAMOUR, JR.[3]

ABSTRACT

Control-pollinated interspecific hybrids between *Liquidambar styraciflua* and *L. formosana* and between *Liriodendron tulipifera* and *L. chinese* were verified by comparison of isoperoxidase banding patterns developed by starch gel electrophoresis of cambial extracts.

The relationships between some of the trees of eastern Asia and eastern United States (Li, 1952) are especially evident in *Liriodendron*, in which the only two species, the American *Liriodendron tulipifera* L. and *Liriodendron chinese* Helmsley, occur in these regions. There are only four species in *Liquidambar*: *Liquidambar styraciflua* L. occurs in eastern United States, with disjunct populations in Mexico and Central America, and *Liquidambar acalycina* and *Liquidambar formosana* Hance are native to China. A fourth species is found in Turkey.

These two genera were among the first to be investigated after the initiation of a project on cytogenetics, breeding, and improvement of landscape trees at the U.S. National Arboretum in 1967. Santamour (1972a) reported successful crossing among three *Liquidambar* species, using leaf morphology to verify interspecific hybridity. Because verification of young hybrids would be more difficult in *Liriodendron*, in which leaf shape of the two species is very similar, Santamour used the biochemical evaluation of leaf flavonoids (Santamour, 1972b) to establish the true hybridity of seedlings from crosses of *L. chinese* made in 1970. This was thought to be the first controlled hybridization between these species.

However, similar research in China was unknown in the West. According to the Nanjing Technological College of Forest Products (1980), they and the Jiangsu Institute of Botany had successfully crossed the two tuliptrees first in 1963, and then several times between 1963 and 1980. They also reported that the hybrids were superior in growth to *L. chinese* at 12 years of age.

In addition, Huang and Chen (1979) verified both natural and artificial interspecific hybrids by analyses of isoenzyme banding patterns from dormant bud extracts. They found that by acrylamide gel electrophoresis of peroxidase isoenzymes they could distinguish the hybrids that contained the isoenzyme bands of both parents as well as two new bands. Inasmuch as our joint research efforts at the U.S. National Arboretum involved considerable work in isoenzyme electrophoresis, we decided to investigate the potential of using this technique to verify the *Liquidambar* and *Liriodendron* hybrids produced at the U.S. National Arboretum and the *Liriodendron* hybrids produced in China.

MATERIALS AND METHODS

All of the parent trees and the progenies derived from controlled crosses at the National Arboretum were available for study. The first material received from China included dormant twigs from one tree each of the parent species and one putative hybrid. A second shipment contained dormant twigs from three putative hybrids.

Although most isoenzyme studies in plants have utilized leaf tissue, Santamour and Demuth (1980) found that cambial tissue was equally as effective for isoperoxidases. Furthermore, studies of cambial isoenzymes can be made at any time of the year and dormant twigs can be shipped halfway around the world with no adverse effects.

The methods used for starch gel electrophoresis and staining of cambial peroxidase isoenzymes were the same as those reported by Santamour (1982) and have been successful in a wide range of woody genera (Santamour & Demuth, 1980, 1981).

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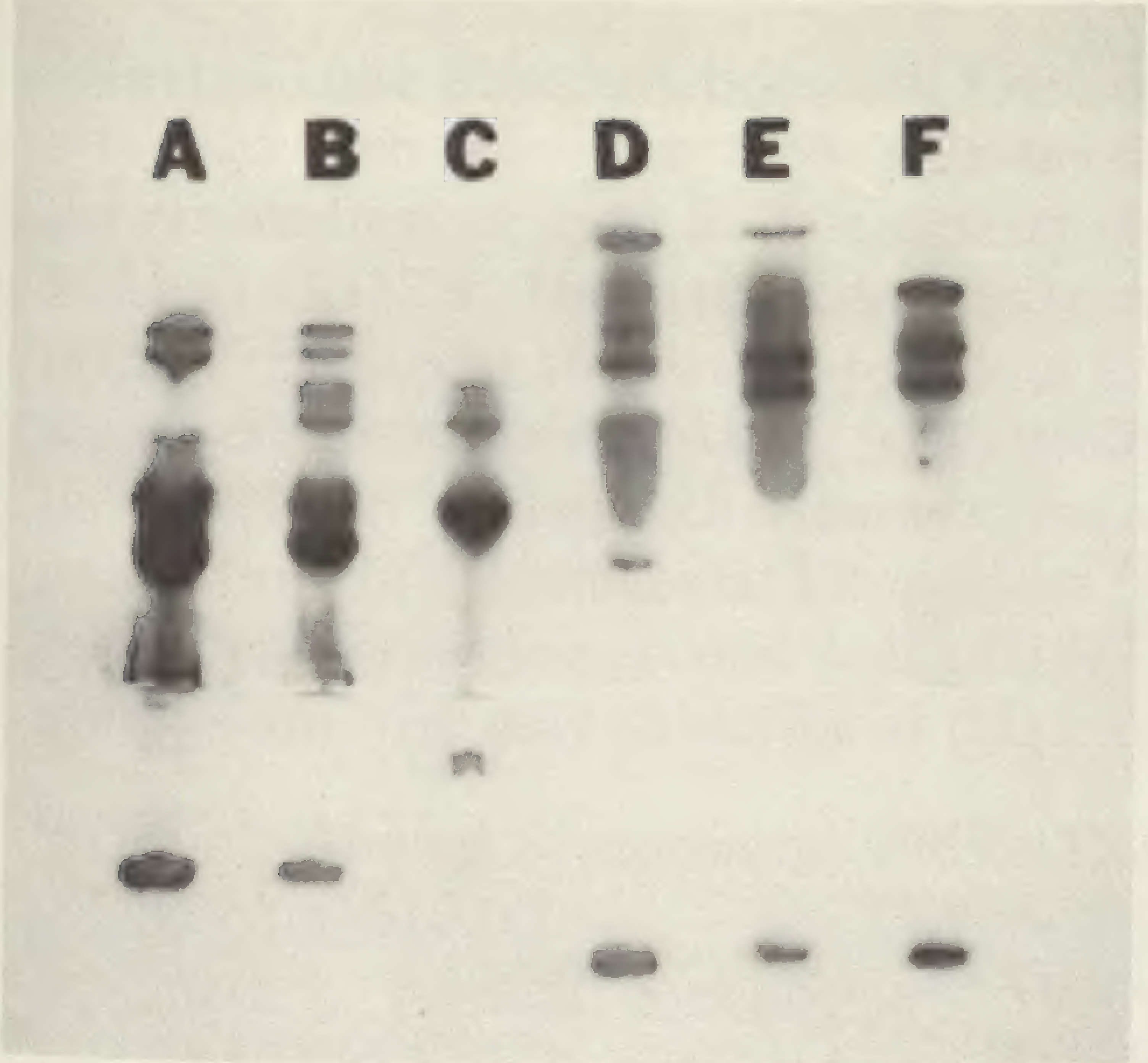

FIGURE 1. Cambial peroxidase banding patterns in (A) *Liriodendron chinese,* (B) *Liriodendron tulipifera* × *Liriodendron chinese,* (C) *Liriodendron tulipifera,* (D) *Liquidambar formosana,* (E) *Liquidambar styraciflua* × *Liquidambar formosana,* and (F) *Liquidambar styraciflua.*

RESULTS AND DISCUSSION

Isoperoxidase banding patterns of cambial tissue of parent trees and hybrids in *Liquidambar* and *Liriodendron* are shown in Figure 1. The interspecific hybrids showed many, but not all, of the bands found in the parent trees, but the hybrids were easily distinguished. The lack of some parental bands in the hybrids might be expected in view of our lack of knowledge concerning the nature and dominance of the genes involved. Houston and Hood (1982) were able to determine the inheritance patterns of only six of the 13 peroxidase isoenzyme bands they found in leaf tissue of tuliptrees, and those were governed by a single pair of alleles.

With cambial isoperoxidases, it is important that the original parents be used in comparison to the hybrids, and not just an individual of the parent species. We found that it was impossible to verify the tuliptree hybrids created in the People's Republic of China by cambial isoenzymes because the parent trees were not available for study. However, as Huang and Chen (1979) noted, the hybrids could be verified by dormant bud analysis. We also analyzed dormant buds of the Chinese material, and although we could distinguish hybrids, the isoenzyme bands were not very clear.

The use of cambial peroxidase isoenzyme banding patterns is an acceptable method for verifying interspecific hybrids in the cases studied here, especially when material of both parents is also available for study. Our work in *Acer* (Santamour, 1982) and *Quercus* (Santamour & Demuth, 1981) has shown that species belonging to the same infrageneric botanical category, which are potentially sexually compatible, frequently have similar patterns of isoenzyme variation. Thus, an individual of one species may or may not possess a different banding pattern than an individual of another species. Two individuals of the same species, however, may have sufficiently different banding patterns that would allow the detection of intraspecific hybrids between them.

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Systematics Symposia Published

In 1953 the Missouri Botanical Garden began holding a series of annual systematics symposia each fall. Since 1969, with the sixteenth symposium, the Garden has published the proceedings of most in its quarterly series, ANNALS OF THE MISSOURI BOTANICAL GARDEN. Those published symposia which are available are listed below, and the price of all except the twenty-fourth is $10.00. The twenty-fourth, which was reprinted separately from the ANNALS, is available for $6.00. Many of these symposium issues of the ANNALS contain other papers, but each issue listed below contains the complete proceedings of the particular symposium. The proceedings of the 1981 symposium will be published during the second half of 1982, and if you wish to purchase a copy of that symposium, you may subscribe at this time. Upon publication, your copy will be sent.

Sixteenth Annual Symposium, 1969—TROPICAL ISLAND BIOGEOGRAPHY. 56(3). 127 pp. $10.00.

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